

A revision of the Australian fossil species of *Zoila* (Gastropoda: Cypraeidae)

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Abstract

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Zoila Jousseaume, 1884 is a cowry genus, the species of which are now confined to the coastal waters of Western Australia and southern Australia. Six fossil species are known from southeast Australia, of which three are new, ranging in age from late Oligocene to middle Miocene, known from the Murray, Otway and Bass basins. Three fossil species are known from Western Australia, of which three are new, ranging in age from late Eocene to late Pliocene, known from the Carnarvon, Bremer and Eucla basins. *Umbilia* (*Gigantocypraea*) Schilder 1927 (type species *Cypraea gigas* McCoy) is regarded as a synonym of *Zoila*. The earliest record of the genus is *Z. chathamensis* (Cernohorsky, 1971). Paleocene/early Eocene, Chatham Islands, probably ancestral to the Australian fossils. *Zoila* is closely related to *Cypraeorbis* Conrad, 1865, of which *Bernaya* Jousseaume, 1884 is regarded as a synonym. Living species are known to have no planktotrophic larval stage, so there is considerable variation in species morphology. Such direct development arose in these cowries at least as early as the late Eocene. Fossils described here are *Zoila viathomsoni* sp. nov., *Z. didymorhyncha* sp. nov., *Z. glomerabilis* sp. nov., *Z. dolichorhyncha* sp. nov., *Z. mulderi* (Tate, 1892), *Z. platypyga* (McCoy, 1876) (= *consobrina* McCoy, *toxorhyncha* Tate, *platypyga simplicior* Schilder), *Z. gigas* (McCoy, 1867) (= *dorsata*, *gabrielii*), *Z. campestris* n. sp. and *Z. fodinata* n. sp.

Keywords

Gastropoda, Cypraeidae, cowries, Australia, Tertiary, new species, taxonomy

Introduction

Zoila is a member of a group of Australian cowries that includes *Notocypraea*, *Umbilia* and *Austrocypraea*, the members of which all seem to have direct larval development rather than having a planktotrophic larval stage as in most species of cowry (Wilson, 1985; Wilson and Clarkson, 2004). This paper reports research results that continue from a study of the Australian endemic genus *Umbilia* (Darragh, 2002).

Subfamily classification

The genus *Zoila* is usually placed in the subfamily Bernayinae Schilder, 1927 erected for the fossil genus *Bernaya* Jousseaume, 1884, of which *Zoila* Iredale, 1935 is a synonym (Wilson and Clarkson, 2004). Meyer (2003), in his work on molecular systematics of cowries, retained most of the subfamilies previously used by many authors on the family, but did not place the genus *Zoila* in any subfamily (although his Table 3 could imply a placement in the subfamily Bernayinae). However, following further molecular work, he subsequently (Meyer, 2004) placed the genera *Zoila* and *Barycypraea* within the subfamily Bernayinae. Cypraeorbinae Schilder, 1927 was erected for the fossil genus *Cypraeorbis* Conrad, 1865. I consider that *Bernaya* is a synonym of *Cypraeorbis*, as argued below. Therefore, if subfamilies are regarded as useful

in classification, Cypraeorbinae should be used instead. Bouchet and Rocroi (2005) included the subfamilies Bernayinae and Cypraeorbinae, along with three other subfamilies, within the synonymy of Gisortinae Schilder, 1927, erected for the genus *Gisortia* Jousseaume, 1884. Species of *Gisortia* have an obsolete fossula, quite different from those of species of *Cypraeorbis* and *Zoila*, so this synonymy is unlikely.

Nomenclatural history of *Zoila* fossil species

The genus *Zoila* was established by Jousseaume (1884a) for three species of large living cowries from Western Australia. The first fossil species later assigned to this genus were described by Frederick McCoy from the Tertiary of Victoria. *Cypraea gigas* was described by McCoy in 1867 without illustration and in 1875, it was redescribed, figured and placed in the subgenus *Aricia*. Two more species, *Cypraea* (*Aricia*) *platypyga* and *C. (A.) consobrina* were described and figured by McCoy in 1876 and 1877, respectively. In 1890, Tate revised these three species and added another two species, *C. toxorhyncha*, regarded here as a synonym of *Z. platypyga*, and *Cypraea dorsata*, regarded here as a synonym of *Z. gigas*. In 1892, Tate figured a new species *C. mulderi* and described it in 1893, pointing out its affinities with *C. platypyga*. Tate assigned all these species to *Cypraea*. Harris (1897) assigned

C. gigas and *C. platypyga* to the subgenus *Erosaria*, which he regarded as a senior synonym of *Aricia*. In 1912, Chapman described *Cypraea gabrieli*, regarded here as a synonym of *Z. gigas*.

Schilder (1927) erected *Gigantocypraea* as a subgenus of *Umbilia* with *C. gigas* McCoy as the type species. He also placed the other species mentioned by Tate in *Umbilia*. However, in 1930, Schilder raised *Gigantocypraea* to generic status and referred the other species to *Zoila*, but subsequently (Schilder, 1935) reduced *Gigantocypraea* to a subgenus of *Zoila* and added a new subspecies, *Z. (Z.) platypyga simplicior*, regarded here as a synonym of *Z. platypyga*.

Time range and distribution

Living species of *Zoila* are known only from the southern and western coasts of Australia. There are seven recognised species, with distribution ranging from Apollo Bay in Victoria westwards across the southern coast and up the west coast of Western Australia as far north as the West Kimberley district (Wilson and Clarkson, 2004). Fossil species of *Zoila* are more widespread. The earliest known species, recognised by this author, occurred in the Paleocene to early Eocene of the Chatham Islands, New Zealand. This species may have given rise to younger Australian species. The earliest Australian species *Z. viathomsoniae* sp. nov., recorded from the upper Eocene of southwest Western Australia, is probably an ancestor of the younger Australian species of *Zoila*, of which there are two groups: an eastern and a western group. The eastern group is known from southeast Australia, and ranged in age from late Oligocene to middle Miocene. This group is characterised by having prominently developed anterior and posterior canals and does not seem to be ancestral to any living species. The western group is known from Victoria, Western Australia, Indonesia and India, and ranged in age from middle Miocene to Recent.

The oldest known member of the western group occurred in the middle Miocene of Western Australia. It seems to be ancestral to *Z. campestris* sp. nov. from the Pliocene of Western Australia. This species is probably ancestral to some of the living species, in particular *Z. venusta* (Sowerby, 1846). Species somewhat similar to the Western Australian species are found in the Neogene of Indonesia and India. A single species, known from one fragmentary specimen, occurred in the late Miocene of Victoria.

Affinities

Generic distinction among cowries is subject to much controversy. Few features of the shell can be used to characterise species groups, particularly without knowing their anatomy and molecular biology. Even when this information is available, it is not always possible to apply this knowledge to include unequivocally fossil species in groups composed of living species. The fossula is one shell structure that does seem to vary sufficiently to be able to use it to some extent in supraspecific classification, and link fossil and living species.

The Australian fossil cowries treated here have a type of fossular morphology similar to that found in species assigned to

four nominal genera: *Cypraeorbis* Conrad, 1865; *Bernaya* Jousseaume, 1884; *Zoila* Jousseaume, 1884; and *Barycypraea* Schilder, 1927. Of these four, only *Zoila* is based on a living species, and hence can be characterised on the basis of anatomy and genetics, although *Barycypraea* — based on a fossil species — has living representatives. The close morphological relationship between the first three genera was first recognised by Schilder (1926), who placed *Zoila* as a subgenus of *Cypraeorbis* and synonymised *Bernaya* with *Cypraeorbis*. Later, as his subdivisions of the Cypraeidae became smaller, and more genera were recognised on the basis of minor differences, Schilder (1941) placed the three genera in his subfamily Cypraeorbinae, with *Zoila* and *Bernaya* in the Tribe Bernayini, and *Cypraeorbis* in the Tribe Cypraeorbini. Dolin (1991) regarded *Zoila* as a possible subgenus of *Cypraeorbis* in the subfamily Bernayinae. In the present study, specimens of the type species of each of these genera, as well as some other species assigned to them, have been examined to determine possible affinities.

Cypraeorbis, type species *Cypraea sphaeroides* Conrad, 1848, was based on a species occurring in the lower Oligocene of the southwest United States of America. The genus ranges in age from late Eocene to at least early Miocene. The fossula (fig. 1B) of a *C. sphaeroides* specimen from Byram, Mississippi (USNM 498351) is deeply excavated and bounded by a prominent lateral ridge on the anterior side. Posterior to this lateral ridge is a slight notch in the fossula margin. The lateral ridge merges anteriorly with a very weak terminal ridge. Between the first columellar tooth and the terminal ridge there is a wide depression, which extends as a sulcus parallel with the terminal ridge into the fossula. The fossula (figs 1C, 3E–F) of a *Cypraeorbis ventripotens* (Cossmann, 1903) specimen — a species closely related to, if not synonymous with *C. sphaeroides* (MacNeil and Dockery, 1984) — from the upper Eocene, Town Creek, Jackson, Mississippi (Mississippi Geological Survey collection) is large, subrectangular, concave, with a prominent notch at the anterior end of the thickened interior edge. The terminal ridge, like that of *C. sphaeroides*, is weakly developed and runs into the interior of the aperture forming the anterior edge of the fossula as a prominent ridge. A well developed groove or sulcus between the first columellar tooth and the terminal ridge runs parallel to the terminal ridge into the fossula. Specimens of *Cypraea willcoxi* (Dall, 1890) and *Zoila arlettae* Dolin, 1991 from the Early Miocene Chipola Formation of Farley Creek, Florida (MNHN, Paris) were also examined. *Z. arlettae* Dolin has a fossula (fig. 3N) very similar to *C. sphaeroides* and *C. ventripotens*, though larger and with a broader notch. *Cypraea willcoxi* Dall is very close in morphology to *Z. arlettae* and also has a fossula (fig. 3O) similar in structure to *Cypraeorbis sphaeroides* and *C. ventripotens*, hence both *Cypraea arlettae* and *Zoila willcoxi* seem to be better placed in *Cypraeorbis* rather than in *Zoila* as suggested by Dolin (1991).

Petuch (2004) erected two new genera in the subfamily Cypraeorbinae, *Floradusta* (type species *Cypraea heilprini* Dall, 1890, early Miocene, Florida) and *Loxacypraea* (type species *Cypraea chilona* Dall, 1900, early Miocene, Florida). He included in these genera several species that had been included by Dolin (1991) in *Cypraeorbis*, *Zoila*, *Siphocypraea* and *Erronea* (*Adusta*). Petuch stated that a fossula was absent in

species of the two genera. This statement is incorrect, as shown by the descriptions and illustrations in Dolin and by my own observations of two of the species, *Cypraeorbis arlettae* and *C. wilcoxi* (see figs 3H–J, N, K, O). Revision of American taxa is beyond the scope of this paper, but I consider that *Floradusta* and *Loxacypraea* are synonyms of *Cypraeorbis*, as the type species of each have a fossula similar to *C. sphaeroides* and *C. ventripotens*. Some of the other species included in *Floradusta* by Petuch (2004) are unlike species of *Cypraeorbis* in that the fossula is crossed by extensions of the columellar teeth and therefore cannot belong in the Cypraeorbinae. These species are best left in the genera to which they were assigned by Dolin (1991).

Bernaya, type species *Cypraea media* Deshayes, 1835, was based on a species from Valmondois in the Paris Basin, Sables Moyens, Bartonian (late Eocene). The differences between *Cypraeorbis* and *Bernaya* are very slight. The fossula of specimens of *Bernaya media* (Deshayes) (figs 1A, 4B, F) from Bois du Roi, Auvers (MNHN), is large, subrectangular and concave. On the interior side, it is bounded by a prominent lateral ridge, in which there is a prominent anterior notch. The terminal ridge of the anterior canal extends into the interior of the aperture and merges with the lateral ridge of the fossula. A well-developed groove adjacent to the terminal ridge runs down into the fossula. This groove is partly obstructed by a columellar tooth, which merges with the terminal ridge. Specimens of *Cypraea bartonensis* Edwards, 1854 from Barton, Hampshire, England (NMV P310165-6) have a similarly structured fossula, but there are no columellar teeth obstructing the groove. In this respect, it closely resembles *Cypraeorbis ventripotens*. A specimen of *Cypraea splendens* Grateloup, 1827, from the Rupelian of Gaas, Landes, France (NMV P310168) also has a fossula identical to *C. ventripotens*.

MacNeil and Dockery (1984) described the protoconch of *C. sphaeroides* as having five whorls, some of which are sculptured with a fenestrate pattern. Dolin and Dolin (1983) have described and figured (figs 3 and 4) the protoconch of *Bernaya media* as having four whorls, which have a fenestrate sculpture on the last two whorls. This form of protoconch suggests a planktotrophic larval stage. As there are no significant distinguishing features between the two genera, it seems appropriate to synonymise *Bernaya* with *Cypraeorbis*.

The type species of *Zoila* is *Cypraea friendii* Gray, 1831, from the waters off Fremantle, Western Australia. Specimens of this species have a large spoon-shaped, deeply concave fossula (Wilson and Clarkson, 2004, pl. 47). The terminal ridge is not prominent, if at all present (on some specimens it is merely represented by a blunt thickening), and there is no prominent ridge bounding the edge of the fossula. There is also no groove running from the ventral surface down into the fossula, though there may be a gap between the labial teeth representing such a groove. There is no notch on the internal edge of the fossula. In these respects, it is unlike the American and European species; however, other species of Australian *Zoila* do have these features, but the edge of the fossula is not markedly notched, rather, merely indented (figs 1E–G).

The fossula in *Zoila chathamensis* (figs 1H, 5I–J) is weakly developed, smooth, broad, very slightly concave, slightly

projecting, and bounded by a very weak terminal ridge. It resembles the fossula in *Z. didymorhyncha* sp. nov. Specimens of *Zoila viathomsoni* sp. nov. have a well-developed fossula (figs 1D, 5L) bounded by a prominent ridge and with a very weak indentation towards the anterior end. There is a very shallow sulcus running into the fossula. Specimens of *Zoila platypygga* (McCoy) have a fossula somewhat similar to *Z. friendii* but the edge of the fossula is more ridge-like. There is no sulcus extending into the fossula parallel to the terminal ridge. Specimens of *Z. didymorhyncha* sp. nov. (figs 1E, 6C) have a weak terminal ridge merging with the edge of the fossula and a shallow sulcus running parallel to it into the fossula. None of the Australian fossils have the well-defined fossular margin or the well-developed notch behind it that is present in the European and American species of *Cypraeorbis*.

Unlike the protoconchs of *Cypraeorbis* species, the protoconchs of species of *Zoila*, where known, are paucispiral, slightly tilted and smooth (Ranson, 1967, pl. 6, figs. 1–3; Wilson, 1998). The protoconch of *Z. platypygga* consists of one whorl slightly tilted from the axis of the shell. The protoconch of *Z. gigas* (McCoy) consists of two whorls, the first of which is irregular and granulated (figs 13E–F). In cross-section (figs 2A–C), the protoconchs of *Z. viathomsoni*, *Z. platypygga* and *Z. gigas* resemble cross-sections of protoconchs of *Umbilia* species (Darragh, 2002, fig. 1). This morphology suggests a protoconch formed from a partly chitinous whorl. Wilson (1985) has shown that living species of *Zoila* have direct development. The protoconchs of the fossils suggest that the fossils also had direct development and that the change from planktotrophic development to direct development had taken place by the late Eocene. Unfortunately, the protoconch of the earliest known species, *Z. chathamensis*, is unknown. *Zoila* species have direct larval development like the other Australian cowries referred to the genera *Austrocypraea* Cossmann, 1903, *Umbilia* Jousseaume, 1884 and *Notocypraea* Schilder, 1927. The last three genera are endemic to Australia and do not have a distribution in shallow tropical seas, whereas species of *Zoila* are known from tropical as well as temperate waters and also have been found in the lower Tertiary of New Zealand, and the upper Tertiary of Indonesia and India. *Austrocypraea*, *Umbilia* and *Notocypraea* seem to be representatives of an ancient southern group, whereas the distribution of *Zoila* suggests that its origin may have been Tethyan. Most tropical cowries are known to have planktotrophic larvae, which accounts for their widespread distribution in the Indo-Pacific realm. *Zoila* seems to have evolved from the widespread genus *Cypraeorbis*, whose species almost certainly had planktotrophic larvae, although the occurrence of a species of *Zoila* in the Chatham Islands as early as the Paleocene to early Eocene may suggest a southern origin.

Though the differences between the genera are slight, *Zoila* seems sufficiently different from *Cypraeorbis* to be maintained for the present. Wilson and Clarkson (2005) suggested that *Zoila* evolved in Asian waters from a directly developing Tethyan ancestor of the subfamily Bernayinae and migrated to Australia in Miocene time. However, the occurrence of species in Australia in the late Eocene and in the New Zealand region in the Paleocene/early Eocene suggests that *Zoila* evolved much earlier, probably from *Cypraeorbis* or some other closely related

taxon, such as *Protocypraea* Schilder, 1927, in the earliest Tertiary or even in the late Cretaceous. Species of *Cypraeorbis* (recorded as *Bernaya*) and *Protocypraea* have been recorded from the upper Cretaceous of North America by Groves (1990, 2004) and *Protocypraea* is also known from the upper Cretaceous of India and the Paleocene of Pakistan (Cox, 1930).

Schilder (1927) erected *Barycypraea* as a subgenus of *Zoila* with type species *Cypraea* (*Aricia*) *caputviperae* Martin, 1899 (probably a synonym of *Cypraea murisimilis* Martin, 1879) for a group of cowries known from the upper Tertiary of Indonesia and living in the Indian Ocean. Molecular biological studies of cowries by Meyer (2004) showed that the nearest living relatives of the Australian living *Zoila* species are the western Indian Ocean species of *Barycypraea* and he grouped both genera in the subfamily Bernayinae. He included no other living taxa in this subfamily. Species of *Barycypraea* have a similar fossula (fig. 3L) to *Zoila* species and they are known to be spongivores like *Zoila* (Liltved, 1989). Species of *Barycypraea* occur in South Africa, Pakistan, India and Indonesia, and range in age from Miocene to Recent (Kay, 1990). The morphology and biogeography of *Barycypraea* suggests an origin similar to that of *Zoila* and a probable common ancestry.

Terminology and repositories

Measurements are given as follows: L = total length of shell; W = width of shell; H = height of shell. Tooth counts are cited as LT = labral teeth and CT = columellar teeth. The terms left and right refer to the animal's true left and right sides, respectively.

All material used in this study, unless otherwise stated, is held in the collections of Museum Victoria, registration numbers with prefixes P (invertebrate palaeontology collection) and F (living mollusca collection). Localities are cited where possible using the Museum Victoria fossil locality register with prefix PL (listed in Beu and Darragh, 2001). Museum acronyms used for other material are as follows: BM(NH) = Natural History Museum, London; SAM T = Tate Collection, South Australian Museum, Adelaide; AMNZ = Auckland Museum, New Zealand; AM C = Australian Museum, Sydney, New South Wales; WAM = Western Australian Museum; USNM = Smithsonian Institution, National Museum of Natural History; MNHN = Muséum national d'Histoire naturelle, Paris; GNS TM = GNS Science (New Zealand).

All specimens figured were coated with ammonium chloride for photography, unless stated otherwise.

Class Gastropoda

Family Cypraeidae Rafinesque, 1815

Subfamily Cypraeorbinae Schilder, 1927

Zoila Jousseaume, 1884

Zoila Jousseaume, 1884a:14.— Jousseaume, 1884b:89.— Cossmann, 1903:146, 149.— Thiele, 1929:275.— Schilder, 1935:336.— Schilder and Schilder, 1939:173.— Wenz, 1941:971.— Dolin, 1991:11

(synonymised *Gigantocypraea* Schilder, 1927). — Wilson and Clarkson, 2004:44.

Cypraeorbis (*Zoila*) Jousseaume. Schilder, 1926:378.

Umbilia (*Gigantocypraea*) Schilder, 1927:86 (type species, original designation, *Cypraea gigas* McCoy, 1867, Miocene, Victoria).

Zoila (*Zoila*) Jousseaume. Schilder, 1935:337.— Schilder, 1939:177.

Zoila (*Gigantocypraea*) Schilder. Schilder, 1935:337.— Schilder, 1939:177.— Wenz, 1941:971.

Cypraea (*Zoila*) Jousseaume. Wilson and McComb, 1967:469. — Wilson, 1993:192.

Type species. *Cypraea scottii* Broderip, 1832 (= *Cypraea friendii* Gray, 1831) by subsequent designation Jousseaume (1884b, p. 89), western and southern Australia.

Diagnosis. Shell small (35 mm) to very large (247 mm) in size, highly glazed, varying in shape, elongate-ovate or pyriform or globose, ventrally flattened. Spire whorls usually covered in callus, rarely protruding. Protoconch, where known, consisting of one to two whorls, the first whorl large, somewhat irregular in shape, deviated slightly from shell axis. Anterior and posterior canals deeply incised, usually short, but on some species produced and bounded by weak to prominent lateral flanges. Aperture narrow, sinuous with weakly to strongly developed short to elongate teeth not extending into aperture or onto fossula. Fossula weakly to strongly developed, broad, slightly to deeply concave and bounded anteriorly by a weak to strong terminal ridge; on some species with very weak sulcus parallel and immediately posterior to terminal ridge.

Time range. Late Paleocene/early Eocene–Recent.

Distribution. India (early Miocene), Indonesia (Pliocene–Pleistocene), Western Australia (late Eocene, Miocene–Recent), South Australia (Miocene, Recent), Victoria (late Oligocene–late Miocene, Recent), Tasmania (early Miocene), New Zealand (late Paleocene/early Eocene).

Remarks. Specimens of *Zoila itoigawa* Tomida, 1989 from the late Miocene of Japan are poorly preserved and have not been prepared sufficiently to enable generic assignment.

As I have recognised two groups of species, an eastern and a western group, it could be argued that these should be accorded taxonomic status if there are significant morphological differences to separate them, in which case *Gigantocypraea* could be used for the eastern group. However, I regard these groups as more geographic entities. There are some morphological differences, but I regard them as minor and not of sufficient importance to use as generic characters. Such variations in morphology are to be expected in species that have no pelagic larval stages.

Some species of the eastern group have considerably produced anterior and posterior canals — for example, *Zoila platypyga* (McCoy) and *Z. mulderi* (Tate) — but other species have canals similar to the living species of the western group — for example, *Z. glomerabilis* n. sp. is similar to *Z. venusta* (Sowerby, 1846) or *Z. gendinganensis* (Martin, 1899).

Columellar dentition varies considerably from species to species. In the living species, columellar dentition can vary from strong to weak even within the one species; for example,

Zoila friendi (Wilson and Clarkson, 2004, pp. 79–80). Fossil species of the western group all have prominent columellar dentition. In *Z. fodinata*, the columellar teeth are elongated to form short ridges. In the eastern group, columellar dentition is more highly variable. In *Z. platypyga*, the columellar dentition is in the form of strong, elongate ridges, whereas in *Z. mulderi* (Tate) (almost certainly ancestral to the former), the columellar dentition is more like that of the living species, as is the dentition of *Z. glomerabilis* sp. nov. and *Z. dolichorhyncha* sp. nov. In *Z. gigas*, there is no columellar dentition. I do not consider that columellar dentition can be used to provide a consistent taxonomic character to separate the eastern and western group of species of *Zoila* as implied by Wilson and Clarkson (2004, p. 49).

Fossular morphology also varies somewhat, though the basic pattern throughout all the species is the same — that is, broad, concave and bounded by the terminal ridge. Even within a species, fossular morphology can vary. Compare, for example, the fossulae of specimens of *Z. venusta* figured on plates 265–276 of Wilson and Clarkson (2004).

Zoila chathamensis (Cernohorsky, 1971)

Figures 1H, 5A, D–G, I–K

Bernaya chathamensis Cernohorsky, 1971, p. 117, fig. 13.

Description. Shell of small size for genus (36 mm), solid, somewhat globose to subpyriform, dorsal surface uniformly convex, ventral surface weakly convex, almost flat. Posterior canal narrow, barely projecting, deeply incised; anterior canal very short, deeply incised. Spire not visible. Outer lip with 14–16 teeth, columella lip with 12–18 teeth. Fossula well developed, smooth, broad, very slightly concave, slightly projecting, bounded by very weak terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype AMNZ TM-1325	35.8	27.3	21.1	18.0	14.0
Figured specimen GNS TM8792	36.5	21.0	21.0	12.0	16.0

Type locality. Flowerpot Harbour, Pitt Island, Chatham Islands, New Zealand, Red Bluff Tuff, late Paleocene/early Eocene.

Occurrence and material. Pitt Island, New Zealand: Red Bluff Tuff, Flowerpot Harbour (holotype AMNZ TM-1325), (GNS GS12159, one specimen); Red Bluff Tuff, GS12173 Rocky side, Tarawhenua Peninsula (GNS TM8792, one specimen).

Remarks. Cernohorsky (1971) assigned his new species to the genus *Bernaya*, apparently not realising that the fossula of species assigned to that genus has a deep groove at the anterior end. His description of the fossula is quite accurate, but his figure does not show the morphology of the fossula very well, as it was not fully prepared. The holotype is refigured here, but the fossula is not very clear in the illustration (fig. 5I). Another specimen kindly provided by Dr Alan Beu has been more fully prepared and although the aperture is narrow, making photography, difficult the simple nature of the fossula can be seen (fig. 5J). The fossula is somewhat similar to that in *Z. viathomsoni* n. sp. and *Z. decipiens* (E.A. Smith, 1880), but is not as concave.

Although much smaller, the overall morphology of this species is somewhat similar to that of *Zoila friendi thersites* (Gaskoin, 1849). The fossula is relatively shorter and is not as deeply concave as that of the latter species, but is otherwise similar.

Zoila viathomsoni sp. nov.

Figures 1D, 2C, 5B–C, H, L

Description. Shell of small size for genus (19–28 mm in length), pyriform. Spire not visible on most specimens, projecting on one specimen. Posterior canal very short, slightly bent to left. Anterior canal very short, slightly deflected to right. Aperture slightly sinuous; outer lip with about 23–25 teeth present along entire lip; columella with about 23–26 teeth present along entire lip. Fossula well-developed, deep, elongate, projecting, bounded anteriorly by thickened ridge; very weak notch present in inner edge just posterior to anterior ridge; weak terminal ridge joining edge of fossula. First columellar tooth adjacent to terminal ridge, almost blocking shallow sulcus that extends into fossula parallel to terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype WAM 72.296	24.0	16.0	12.5	25.0	26.0 undistorted
Paratype WAM 72.253	27.0	15.0 est.	14.0 est.	c24.0	24.0 distorted
Paratype P310193	28.0	15.0	13.0 est.	24.0	23.0 crushed laterally
Paratype P310194	17.0	11.7 fragment showing fossula			

est. = estimated

Type locality. PL3171 gravel scrape beside Thomson Highway, 23.5 km north of Highway 1, north of Walpole, Western Australia. Grid ref. Deep River (1:100 000 series) 743487. Pallinup Siltstone, Aldingan, Late Eocene.

Type material. Western Australian Museum: Holotype WAM 72.296, collected T.A. Darragh and G.W. Kendrick, 12–14 March 1969; paratype WAM 72.253, collected G.W. and W.E. Kendrick, 25 January 1969. Museum Victoria: Paratype P310193, collected T.A. Darragh & G.W. Kendrick, 12–14 March 1969.

Time range. Aldingan, Late Eocene.

Occurrence and material. Type locality only (one undistorted specimen, four complete distorted specimens, nine fragments).

Remarks. This is one of the two oldest true cowries recorded from Australia and occurs only in southwest Australia, associated with *Willungia ovulatella* (Tate) and *Semitrivia pompholugota* (Tate). Specimens from the type locality are preserved as silica replacements weathered out of the Pallinup

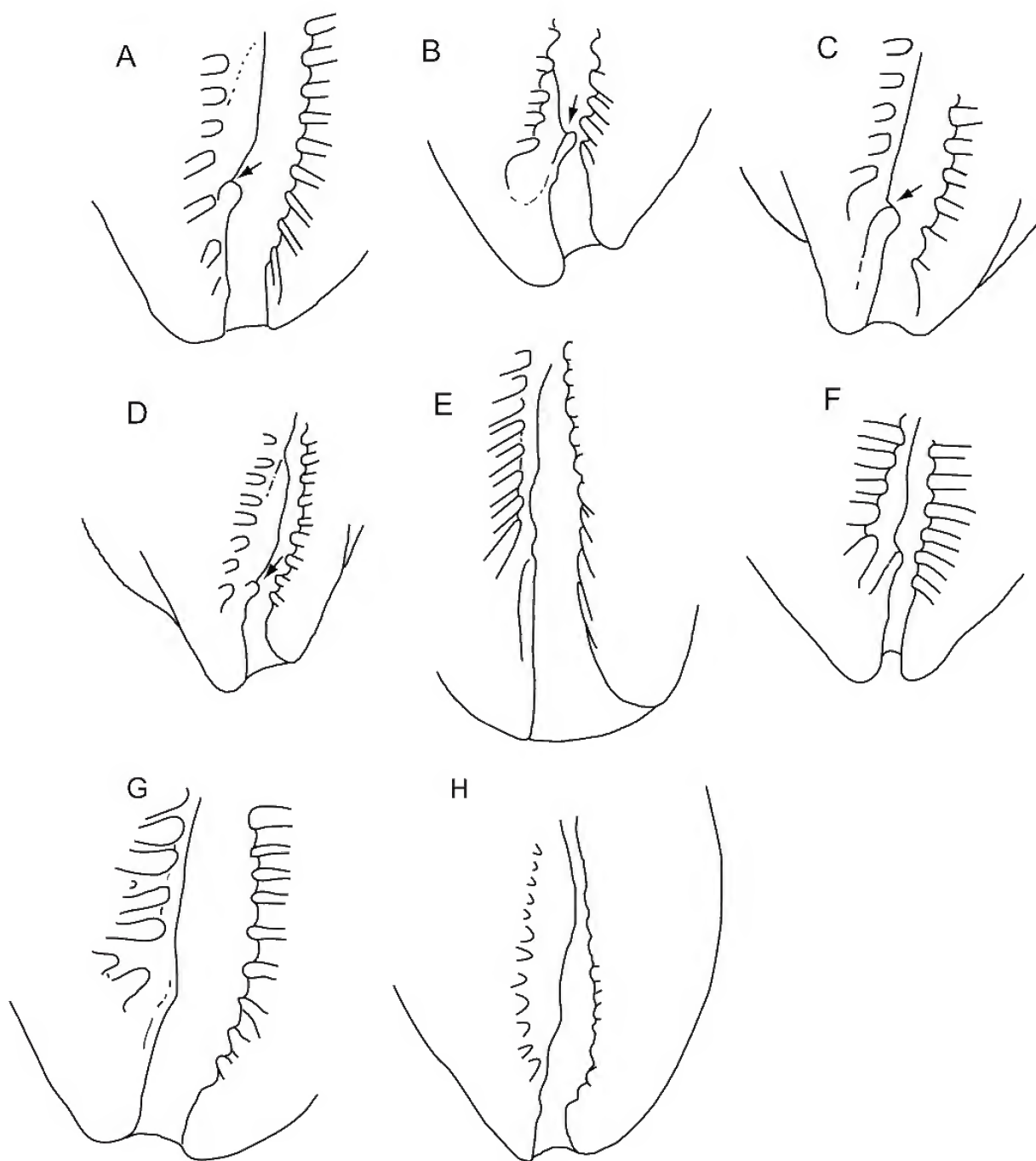


Figure 1. A, *Cypraeorbis medius* (Deshayes, 1835), $\times 5$; B, *Cypraeorbis sphaeroides* (Conrad, 1848), $\times 5$; C, *Cypraeorbis ventripotens* (Cossmann, 1903), $\times 5$; D, *Cypraeorbis viathomsoni* sp. nov. WAM 72.296, $\times 5$; E, *Zoila didymorhyncha* sp. nov. P302687, $\times 2.6$; F, *Zoila campestris* sp. nov. WAM 89.437, $\times 2.6$; G, *Zoila fodinata* sp. nov. WAM 89.637, $\times 3$; H, *Zoila chathamensis* (Cernohorsky, 1971) GNSTM 87922, $\times 2.3$. Arrows indicate the location of the notch.

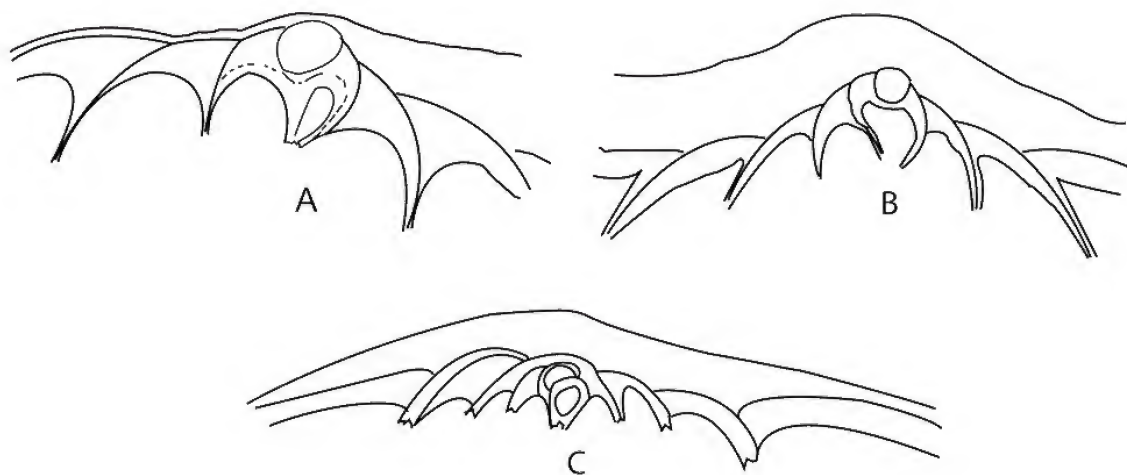


Figure 2. Protoconchs. A, *Zoila platypygma* (McCoy, 1876), P308781, $\times 7$; B, *Zoila gigas* (McCoy, 1867), P308792, $\times 3.6$; C, *Zoila viathomsoni* sp. nov., WAM $\times 10$.

Siltstone. The associated fauna comprises large numbers of siliceous sponges. The protoconch observed in cross-section (fig. 2C), is paucispiral and slightly deviated from the axis of the teleoconch, unlike the multispiral protoconchs of *Cypraeorbis* species. The general size and shape of the shell resembles that of *Cypraeorbis medius*, *C. bartonensis* and *C. ventripotens*; however, the fossula (fig. 5L) is not the same as that present in these species. The fossula is very wide and prominent, projecting into the aperture. It is more elongate than that of these three species, does not have a prominent notch and the anterior border is not thickened. In general shape and concavity, it resembles those in *Zoila friendii* and *Z. decipiens*. *Zoila viathomsoni* bears a close resemblance to *Z. chathamensis* (Cernohorsky), late Paleocene to early Eocene, Chatham Islands, New Zealand, but it is not as tumid, has much finer and more numerous apertural teeth, the posterior labral border of the posterior canal is more produced posteriorly and it is only about two-thirds the size. Given the similarities, *Z. chathamensis* is a possible ancestor of *Z. viathomsoni* sp. nov.; *Z. chathamensis* is the earliest known representative of the genus.

Zoila viathomsoni bears some resemblance in size and shape to *Lyncina* (*Austrocypraea*) *onkastoma* Yates, 2009, recorded from the early Oligocene of South Australia, but lacks the well-defined anterior rostrum of *L. (A.) onkastoma*, as well as the prominent notch on the fossula.

Etymology. Latin via road.

Zoila didymorhyncha sp. nov.

Figures 1E, 6A–E, I

Description. Shell solid, small for genus, elongate, subfusiform; base relatively flat, but rounded on either side of aperture. Spire

not visible. Posterior canal long, with rounded sides, sunk into massive rounded posterior rostrum formed by extensions of inner and outer lips. Anterior canal long, with rounded sides, sunk into a thick, rather flat rostrum. Aperture somewhat sinuous; outer lip with 10–24 well-developed teeth extending along entire lip; teeth completely obsolete on one specimen. Columella lip with 3–26 well-developed teeth extending along entire lip on most specimens; teeth obsolete on one specimen. Fossula moderately developed, very shallow, bounded anteriorly by a small, weak, terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype P302687	62	31	25	24	26
Paratype P302685	80	32	27	10	3
P302686	64+	32	26	22+	25 anterior canal broken

Type locality. PL3022 cliff section at Addiscot Beach, beds B109–107, southwest of small gully, clay overlying Demons Bluff Formation, Victoria. AMG Torquay BT619490. Jan Juc Formation. Early Janjukian.

Type material. Holotype P302687, collected T.A. Darragh, 4 December 1985; paratype P302685, collected T.A. Darragh 8 May 1990.

Time range. Early Janjukian, Late Oligocene.

Occurrence and material. PL3022 Addiscot Beach (three specimens).

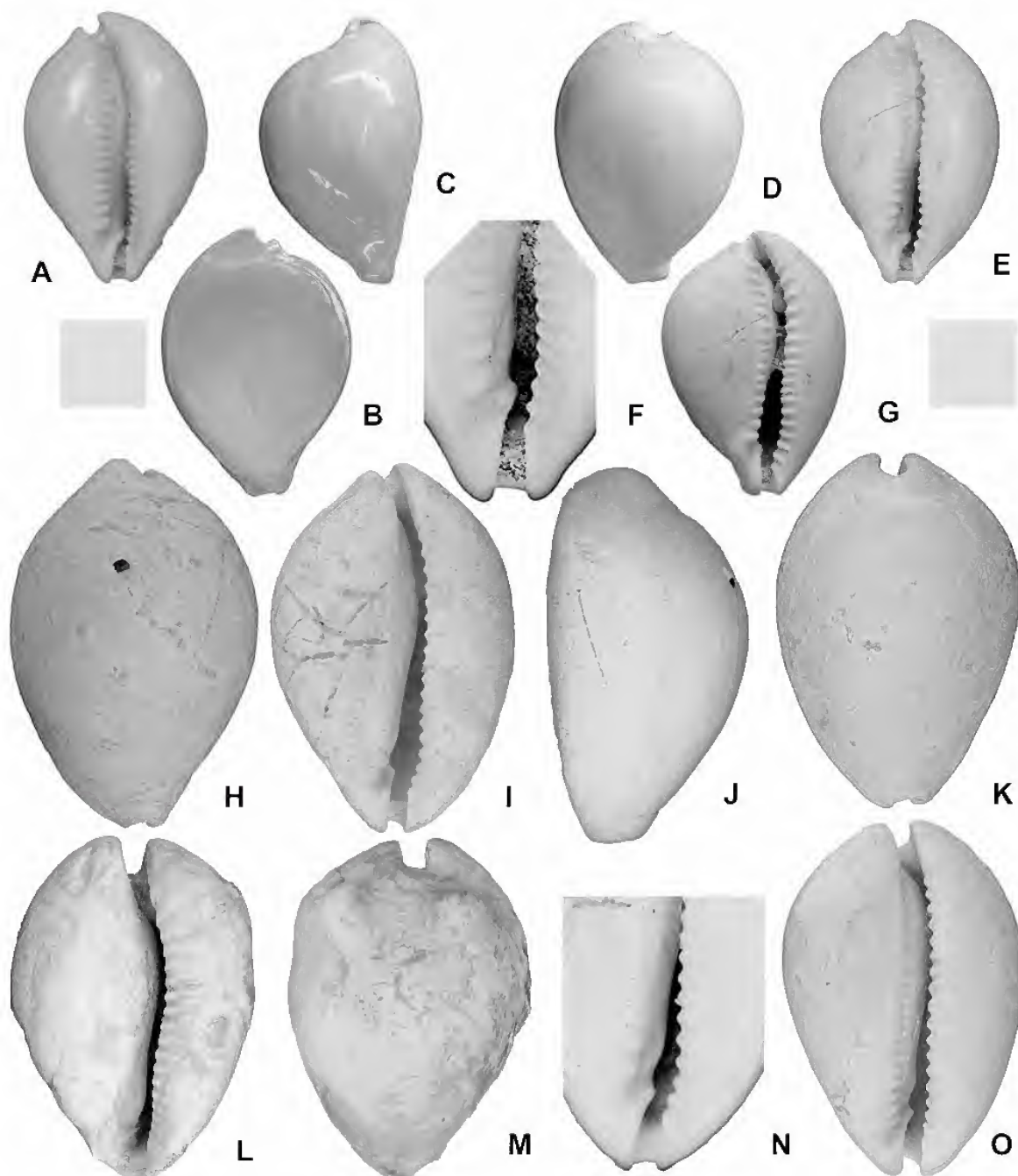


Figure 3. A–G, *Cypraeorbis ventripotens* Moodys Branch Formation, late Eocene, Town Creek, Jackson, Mississippi, United States of America; A–C, $\times 2$; F, $\times 4$; D–E, G, $\times 2$; H–J, N, *Cypraeorbis arlettae* MNHN, Chipola Formation, Burdigalian, early Miocene, Farley Creek, Calhoun County, Florida, USA; K, O, *Cypraeorbis wilcoxi* MNHN, Chipola Formation, Burdigalian, early Miocene, Farley Creek, Calhoun County, Florida, United States of America; L–M, *Barycypraea zietsmani* Liltved and Le Roux, 1988, P31664, Alexandria Formation, late Neogene, Eastern Cape, South Africa, $\times 1$.

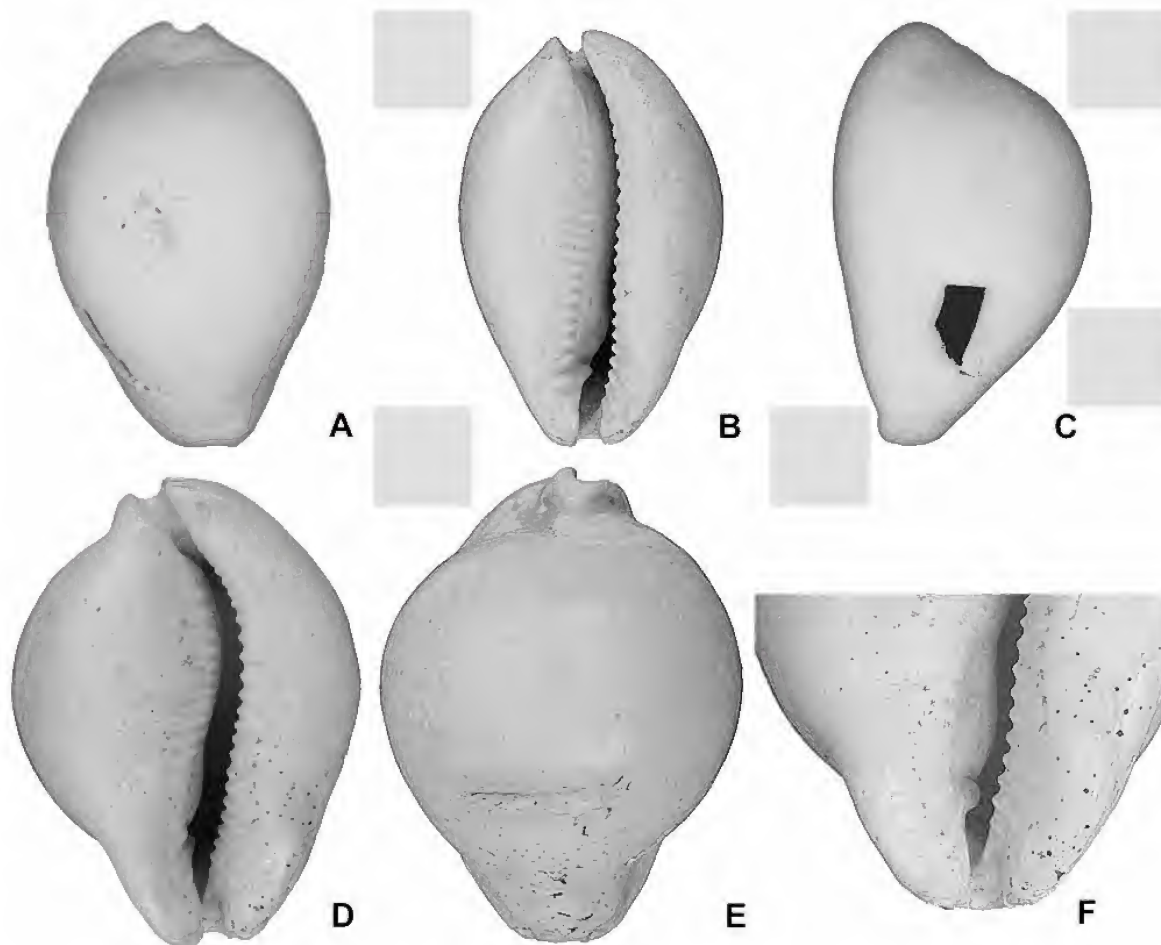


Figure 4. A–F, *Cypraeorbis medius* MNHN, Bartonian, late Eocene, Bois du Rois, Auvers sur Oise, France; A–C, D–E, $\times 1.5$; F, $\times 2$.

Remarks. The small size and the massive development of the anterior and posterior rostra separate this species from all others in the genus. In morphology, it comes closest to *Zoila mulderi* (Tate), but it has a massive anterior rostrum lacking in *Z. mulderi* and the posterior rostrum is not notched as it is in *Z. mulderi*.

Etymology. Greek, didymos, double; rhynchos, snout.

***Zoila glomerabilis* sp. nov.**

Figures 6F–H, 7A–F

Description. Shell of large size for genus, solid, globosely pyriform, abruptly contracted anteriorly to short, narrow anterior canal. Spire projecting slightly, almost entirely enveloped by last whorl, covered with thick callus. Posterior canal short, deeply incised, reflexed to the left. Anterior canal deeply incised, with rounded sides, reflexed dorsally, supported laterally by very short, narrow flanges. Aperture sinuous,

slightly widened and sloping steeply inwards before anterior canal. Outer lip with 28–36 teeth extending along entire lip; inner lip with 15–32 teeth extending along entire lip on most specimens; weaker posteriorly on some specimens and on few specimens extending only along half of lip. Fossula well developed, broad, relatively deeply depressed, bounded anteriorly by weak terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype P14515	96	59	52	35	30
Paratype P308740	85	52	40	35	26
Paratype P315526	80	50	42	33	13

Type locality. Lower beds of section south of Fishermen's Steps, Bird Rock Cliffs, Torquay, Victoria. Jan Juc Formation.

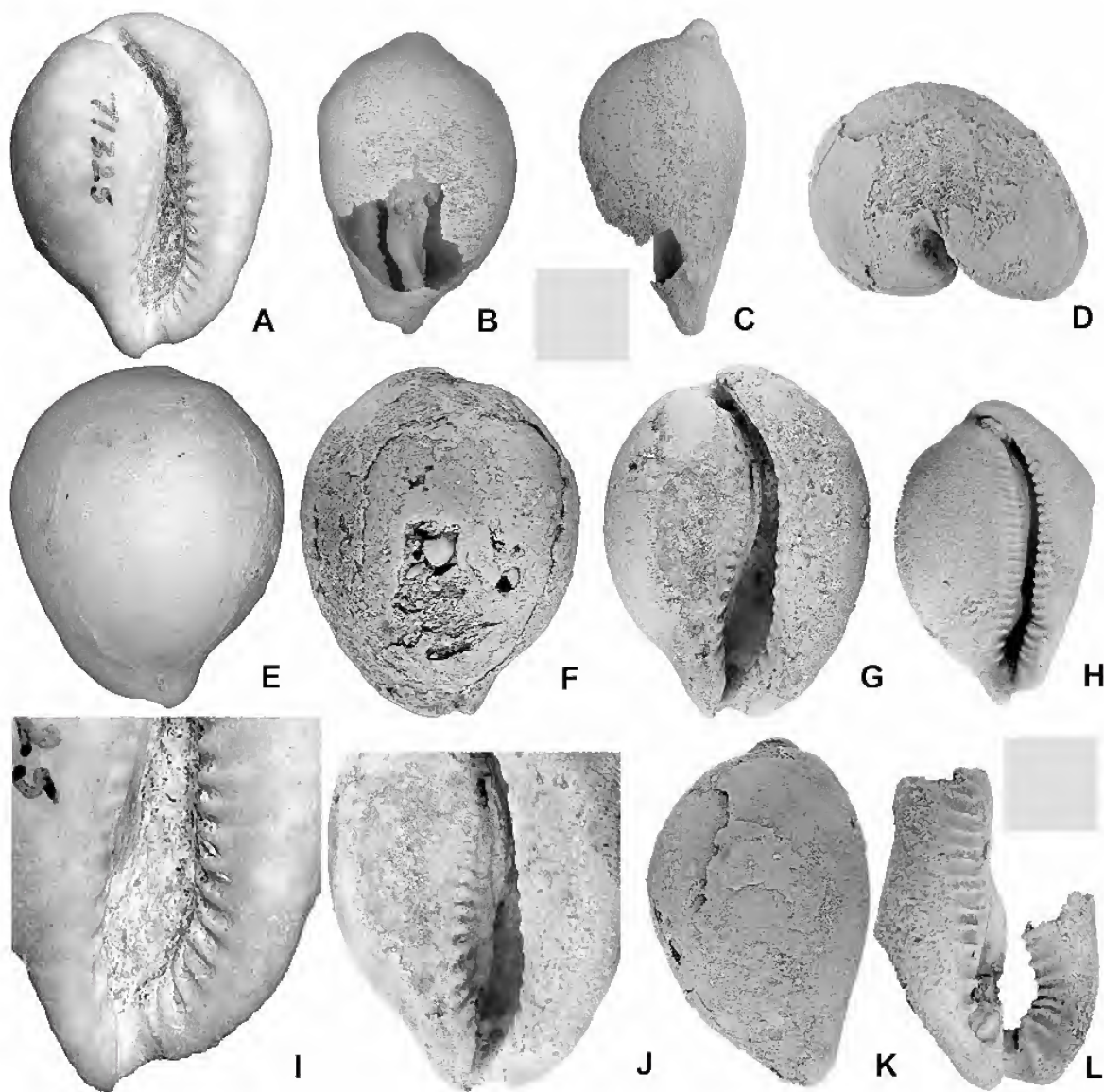


Figure 5. A, D–G, I–K, *Zoila chathamensis*; A, E, I, holotype, AIM 71325, Flower Pot Harbour, Chatham Islands; A, E, $\times 1.5$; I, $\times 2$; D, F–G, J–K, GNS TM8792, Taruwhenua Peninsula, Chatham Islands; D, F–G, K, $\times 1.5$; J, $\times 2$; B–C, H, L, *Z. viathomsoni*; B–C, H, holotype, WAM 72.296, Thomson Highway, Western Australia; L, fossula, P310194, Thomson Highway, $\times 3$.

Type material. Holotype P14515, F.A. Cudmore collection; paratype P308740, presented S. F. Colliver, 16 January 1962; paratype P315526, presented C. Goudey, 2009.

Time range. Janjukian, Late Oligocene–Longfordian, Early Miocene.

Occurrence and material. Janjukian: Jan Juc Formation. At sea level, Bird Rock, Torquay (P304422, one specimen); Half

Moon Bay, Torquay (P315526, one specimen); Torquay (P308706, P304432, P304423, seven specimens); Geological Survey of Victoria locality Ad22, Bird Rock, Torquay (P308717, one specimen).

Longfordian: Fishing Point Marl. ‘Picnic bed’, Horden Vale (P308741–2, two specimens).

Remarks. This species is very similar in morphology to

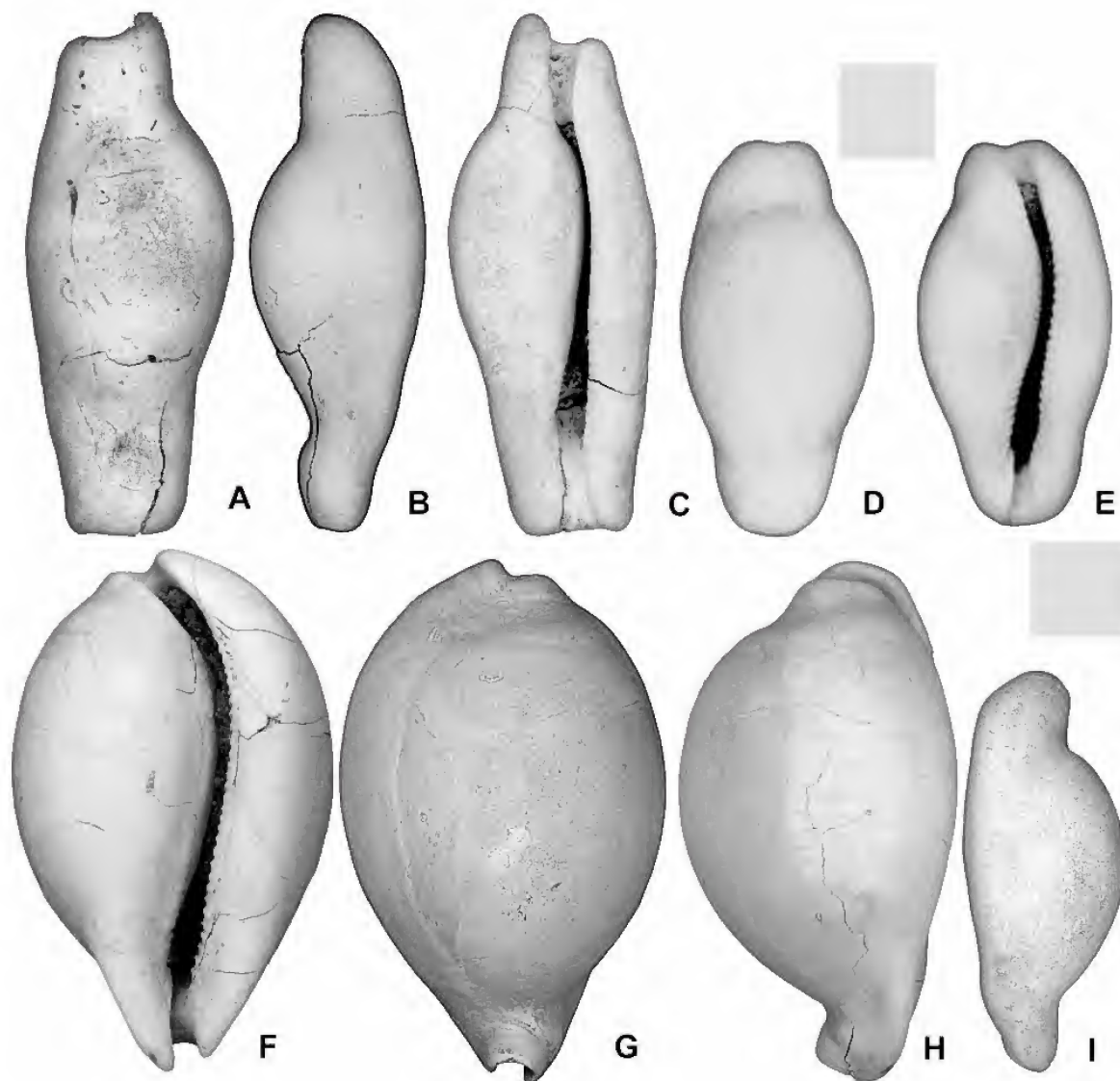


Figure 6. A–E, I, *Zoila didymorhyncha*; A–C, paratype, P302685, PL3022, $\times 1$; D–E, I, holotype, P302687, PL 3022, $\times 1$; F–H, *Z. glomerabilis*, paratype, P315526, Half Moon Bay, Torquay, $\times 1$.

Z. dolichorhyncha sp. nov. but differs in that it is more globose, has a shorter anterior canal and tapers more abruptly towards the anterior. *Zoila glomerabilis* bears some resemblance to *Z. venusta* (Sowerby), Recent, Western Australia, but is more globose and has a prominent anterior canal lacking in *Z. venusta*. The fossula is very similar to that in *Z. venusta*, but not quite as elongate.

Etymology. Latin, *glomerabilis*, round.

Zoila dolichorhyncha sp. nov.

Figures 8A–F, 9C–E

Description. Shell of large size for genus, solid, pyriform, somewhat humped posteriorly and tapering anteriorly, of six teleoconch whorls. Spire projecting slightly, almost enveloped by last whorl, covered with thick callus. Protoconch of one smooth whorl, not differentiated from teleoconch whorls,

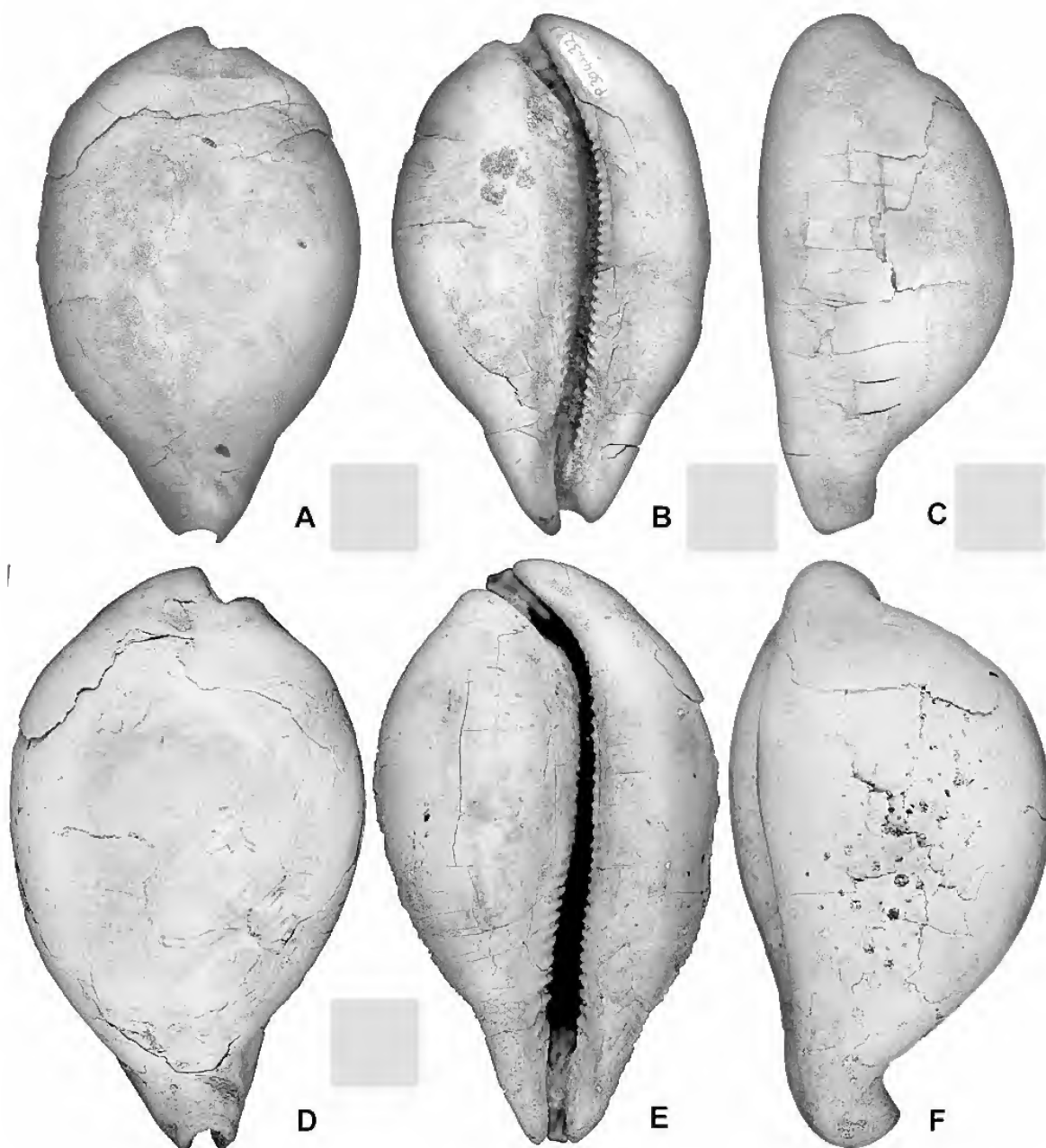


Figure 7. A–F, *Zoila glomerabilis*; A–C, paratype, P308740, Torquay, $\times 1$; D–F, holotype, P14515, Bird Rock cliffs, Torquay, $\times 1$.

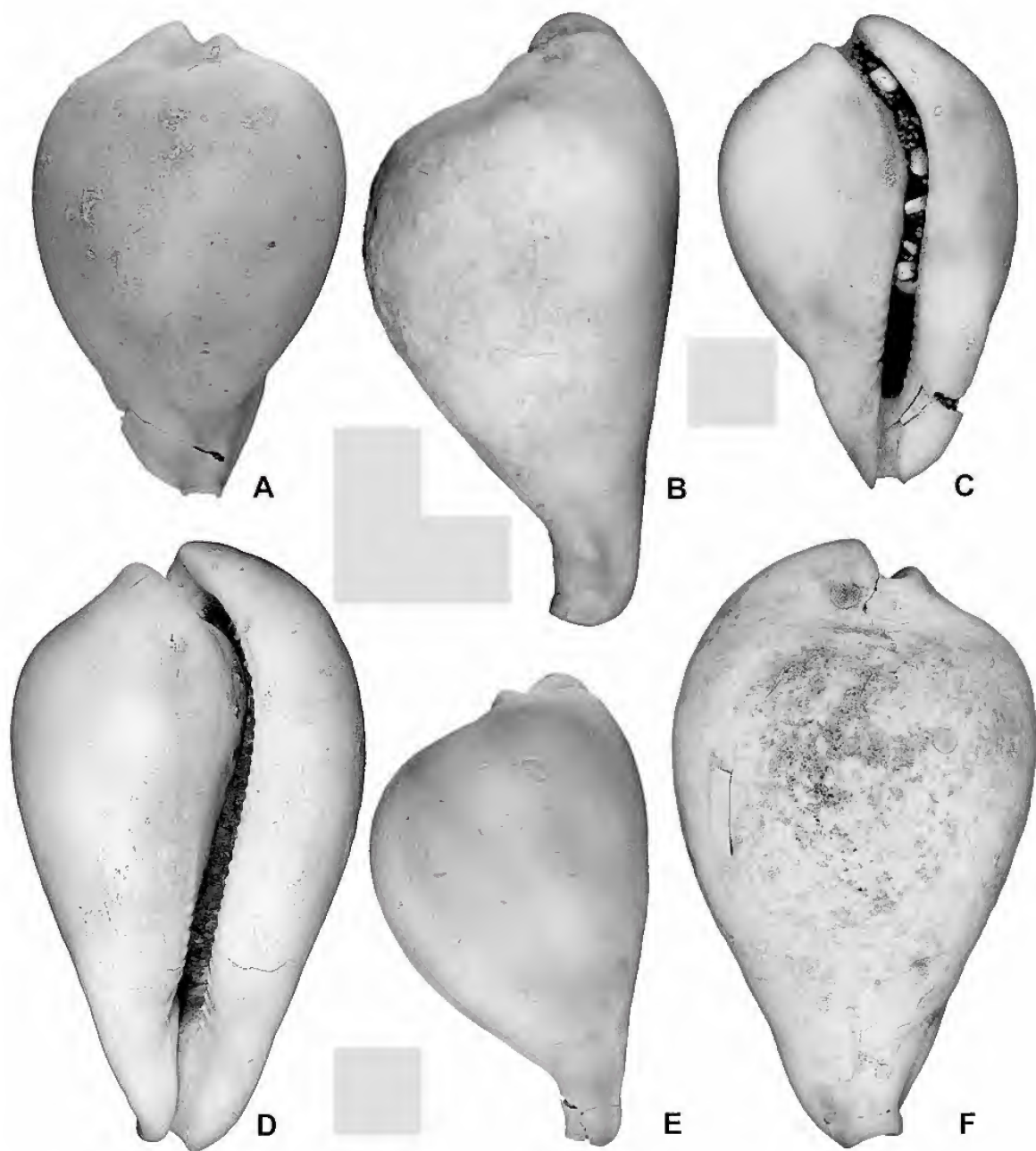


Figure 8. A–F, *Zoila dolichorhyncha*; A, C, E, paratype, P304418, PL3028, $\times 1$; B, D, F, holotype, P14514, PL 3028, $\times 1$.

coiled with the axis of the shell. Posterior canal short, deeply incised, reflexed to left. Anterior canal deeply incised, with rounded sides, reflexed dorsally, supported laterally by short, narrow flanges. Aperture sinuous, slightly widened and sloping steeply inwards before anterior canal; outer lip with 23–33 teeth extending along entire lip, on some specimens becoming very weak posteriorly; inner lip with 3–11 teeth (generally fewer than 10) present on anterior third of lip. Fossula well developed, broad, relatively deeply depressed, bounded anteriorly by weak terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype P14514	101	60	52	33	10
Paratype P304417	81	47	42	26	7
Paratype P304418	79	51	45	24	8

Type locality. Lower bed, Table Cape, Wynyard, Tasmania, (i.e. PL3028 lower bed in cliff between Fossil Bluff and 1.5 km northwest towards Table Cape, Wynyard, Tasmania, Table Cape 930630). Freestone Cove Sandstone, Early Miocene, early Longfordian.

Type material. Holotype P14514, purchased R.N. Atkinson, 8 May 1911; paratypes P304417–8, purchased R.N. Atkinson, 15 January 1910.

Time range. Longfordian, Early Miocene

Occurrence and material. Table Cape (P2644, P14618, P2766–2770, P14595–6, P304417, P304449–50, 11 specimens); *Crassatella* bed, Fossil Bluff (P304440, one specimen); lower bed, Table Cape (P308708, P304431, P304433, seven specimens).

Remarks. This species has been mistaken for *Zoila platypyga* (McCoy) and recorded as such in lists of fossils from Table Cape published by Johnston (1888, p. 262) and Pritchard (1896, p. 106). It probably evolved from *Z. glomerabilis* sp. nov., from which it differs by being pyriform with a tapering anterior rather than being globose. *Zoila glomerabilis* has a uniformly rounded dorsum, whereas *Z. dolichorhyncha* sp. nov. has a dorsum humped posteriorly.

Etymology. Greek, dolichos, long; rhynchos, snout.

Zoila mulderi (Tate, 1892)

Figures 9A–B, 10A–F

Cypraea mulderi Tate, 1892, pl. 9, fig. 2.— Tate, 1893, p. 316 (description).

Gistortia (Palliocypraea) mulderi (Tate).— Vredenburg, 1927, p. 60.

Zoila (Zoila) mulderi (Tate).— Schilder, 1935, p. 337.

Zoila (Gigantocypraea) mulderi (Tate).— Wilson and Clarkson, 2004:52, pl. 56.

Description. Shell solid, of medium to large size for genus, subglobose, covered with glaze. Spire scarcely visible, covered with thick callus. Posterior canal wide, sides rounded, deeply notched dorsally, sides extended posteriorly into prominent thick flanges extending from base. Anterior canal deeply

incised, sides rounded, reflexed dorsally, supported by very thick lateral flanges extending from base. Aperture somewhat sinuous, narrow; outer lip with 24–32 teeth, markedly decreasing in strength at posterior two-thirds. Columella with 9–29 weak, short teeth, present on anterior two-thirds. Fossula weakly depressed, subcircular, bounded anteriorly by weak terminal ridge. Dorsum coarsely dimpled on some specimens.

Dimensions.

	L	W	H	LT	CT
Holotype SAM T822	102	64	49	29	8
Figured specimen P13374	96	60	45	32	11 topotype
Figured specimen P3044471	106	63	49	23+	14 Curlewis

Type locality. ‘In a well sinking at Belmont’. A note by Mulder, dated 1891, with a photograph of the specimen sent to Professor Tate (i.e. the holotype), states that only two specimens were known, one in Mulder’s possession (i.e. P13374) and the other sent to Tate. They were ‘taken from the bottom of a shaft about 60 feet below the surface. The shaft was sunk at Belmont near Geelong’. The shaft was sunk in about 1891 in an effort to find fire clay in a paddock close to the junction of the Colac Road (now Princess Highway) and the Germantown (now Grovedale) Road (now Corio Street), probably in allotment 9, Parish of Barrabool. The site was described by Mulder (1897, p. 23).

Type material. Holotype SAM T822, R. Tate collection.

Figured specimen P13374, collected J.F. Mulder 1891, purchased 1921; figured specimen P3044471, collected F.A. Cudmore, 21 April 1940.

Time range. Longfordian–Batesfordian, Early Miocene.

Occurrence and material. Longfordian. Fishing Point Marl: PL3035 southeast of Fischers Point (P308770, one fragment).

Batesfordian. Fyansford Formation: PL3040 Belmont Shaft (P13374, one specimen). Curlewis (P304416, P304447, P308743, four specimens and three fragments).

Gellibrand Formation: PL3048 Bornong Road cutting (P304421–2, P308767, one specimen and two fragments); PL3163 Williams Road cutting (P310103, one fragment of anterior).

Horizon unknown. Fishing Point Marl? ‘Cape Otway’ (probably Aire River) (P302701, one specimen).

Fishing Point Marl: Fishing Point (P308769, one fragment).

Remarks. The Bornong cutting specimens have the general shape of specimens from Belmont and Curlewis, but have some characters intermediate with *Zoila platypyga* (McCoy) in that the teeth are more strongly developed. The labral teeth extend along the entire lip and the columellar teeth are strongly developed ridges extending along the entire columella as in *Z. platypyga*. This suggests that *Z. mulderi* is ancestral to *Z. platypyga*. The specimen labelled Cape Otway probably came from the upper part of the Fishing Point Marl (Batesfordian) outcropping in the cliffs along the Aire River at Horden Vale.



Figure 9. A–B, *Zoila mulderi* holotype, SAM T822, Belmont, $\times 1$; C–E, *Z. dolichorhyncha*, paratype, P304417, PL 3028, $\times 1$.

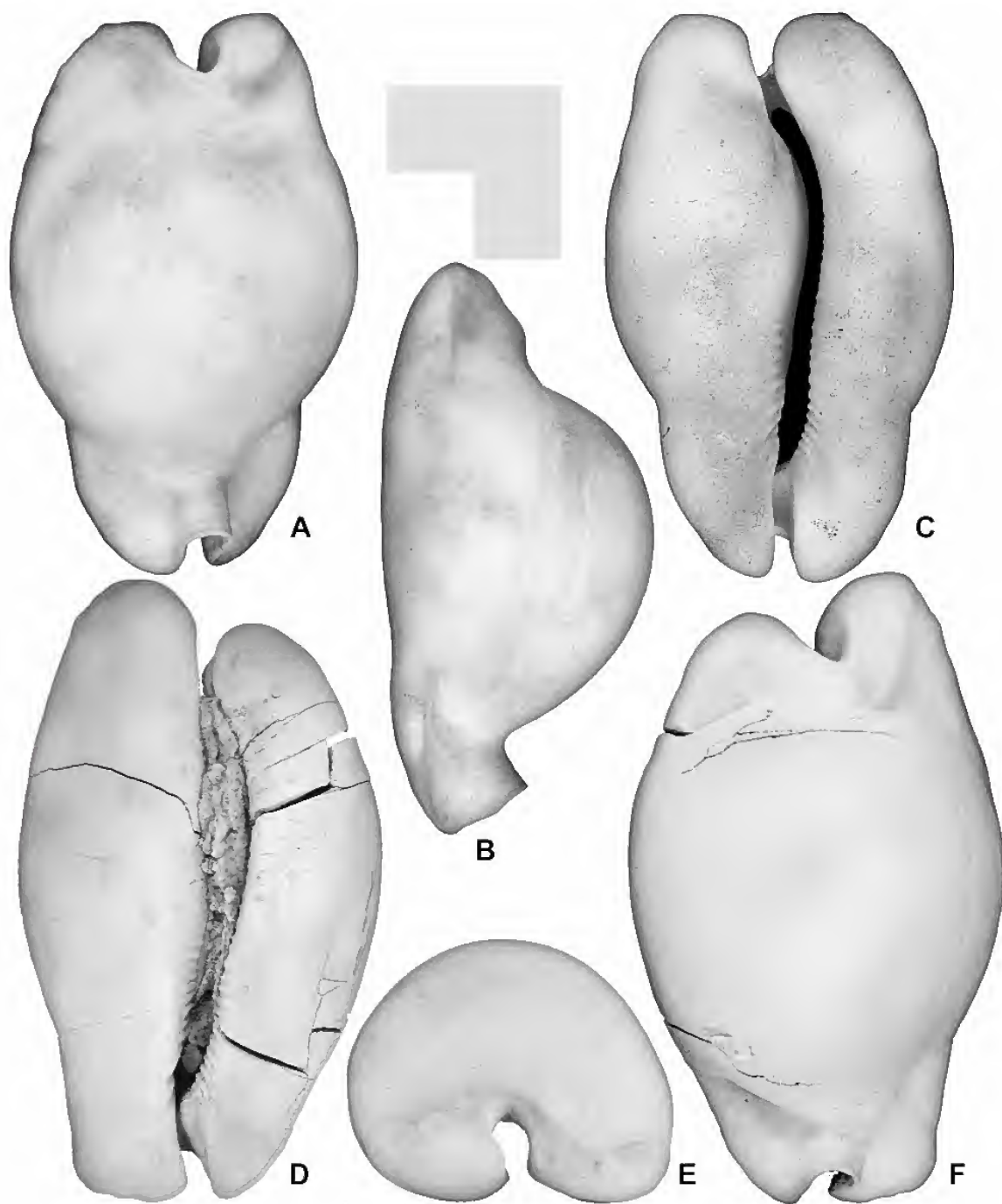


Figure 10. A–F, *Zoila mulderi*; A–C, E, P13374, Belmont, $\times 1$; D, F, P304416, Curlewis, $\times 1$.

***Zoila platypyga* (McCoy, 1876)**

Figures 2A, 11A–H, 12A–G, 13A–C

Cypraea (Aricia) platypyga McCoy, 1876, p. 39, fig. 1–1c.*Cypraea (Aricia) consobrina* McCoy, 1877, p. 36, pl. 49, fig. 2.*Cypraea toxorhyncha* Tate, 1890, p. 210.—Tate, 1892, p. 5, fig. 6; pl. 6, fig. 5.*Cypraea platypyga* McCoy.—Tate, 1890, p. 211.*Cypraea (Erosaria) platypyga* McCoy.—Harris, 1897, p. 209.*Gisortia platypyga* (McCoy).—Vredenburg, 1927, p. 43.*Gisortia consobrina* (McCoy).—Vredenburg, 1927, p. 43.*Zoila (Zoila) platypyga platypyga* (McCoy).—Schilder, 1935, p. 338.*Zoila (Zoila) platypyga simplicior* Schilder, 1935, p. 338.*Zoila (Zoila) consobrina* (McCoy).—Schilder, 1935, p. 338.*Zoila (Zoila) toxorhyncha* (Tate).—Schilder, 1935, p. 338.*Zoila platygyra* [sic] (McCoy).—Wilson and Clarkson, 2004:51, pl. 52, pl. 53 (*toxorhyncha*) form.*Zoila consobrina* (McCoy).—Wilson and Clarkson, 2004:51, pl. 54.

Description. Shell of five to six whorls, solid, of medium size for genus, globose to subpyriform, last whorl covered with glaze, enveloping the previous whorls, somewhat humped posteriorly with posterior dorsal slope steeper than anterior; smooth dorsal surface. Spire slightly projecting, of 4–5 whorls, covered with thick callus on most specimens. Protoconch smooth, of one whorl merging imperceptibly with teleoconch whorls; beginning of protoconch slightly immersed. Posterior canal with rounded sides, wide, notched, projecting posteriorly on most specimens with prominent solid lateral projections, longer on columellar side. Anterior canal subcylindrical, narrow, deeply incised, reflexed dorsally and supported by thick lateral flanges on most specimens; on large specimens canal considerably extended. Aperture narrow, very slightly curved, slightly wider and steeply sloping inwards at anterior end before anterior canal; outer lip with 24–33 well-developed teeth extending along entire lip. Columella with 24–33 strongly developed ridges, extending along entire columella, bifurcating on some specimens, not extending onto fossula. Fossula well developed, concave, broad and spoon-shaped, bounded anteriorly by well-developed single terminal ridge.

Dimensions.

	L	W	H	LT	CT
Holotype P12137	77	49	42	24	27
P12134	67	43	37	30	28 holotype of <i>consobrina</i>
T823	94	47	42	28	26 holotype of <i>toxorhyncha</i>
Figured specimen P304414	100	54	51	33	33
Figured specimen P304415	82	50	41	30	30
Figured specimen P14594	100	53	51	33	26

Type locality. ‘Tertiary clays of shore near foot of Mount Eliza’.**Type material.** Holotype P12137, collected Geological Survey of Victoria. Holotype of *Cypraea (Aricia) consobrina* P12134,

Moorabool River. Holotype of *Cypraea toxorhyncha* Tate, 1890, SAM T832, Muddy Creek, Ralph Tate collection. Holotype of *Zoila (Z.) platypyga simplicior* Schilder, 1935, BM(NH), Muddy Creek, E.O. Teale collection (specimen missing). Figured specimen P304414, F.A. Cudmore collection, collected 1941. Figured specimen P304415, presented Mr J. T. Cunningham, 22 February 1966. Figured specimen P14954, collected F.A. Cudmore, February 1932.

Time range. Balcombian–Bairnsdalian, Middle Miocene.

Occurrence and material. Balcombian. Muddy Creek Formation: Muddy Creek (P14639, P61587, P304426, P308692–4, P308696, P308748, P308798, P308796, 21 specimens); PL3082 Clifton Bank (P58641, P304419, P304434, P304446, P308691, P308695, P308697, 16 specimens).

Gellibrand Formation: Gellibrand River (P304424, P304448, P308734, four specimens); northwest of Princetown (P304441, one specimen); Princetown (P5347, one specimen); PL3060 dam on lot 393 (P304429, one specimen); 4 km north of Port Campbell (P304439, one specimen); between Pt. Ronald and Gibsons Beach (P304444, one specimen); Cowley Creek (P304438, one specimen); dam at Clyne’s house (P308698, one specimen); north of Port Campbell (P308699, one specimen); Curdies (P59228, one specimen); PL3068 southwest end of Gibson Beach (P304443, one specimen).

Fyansford Formation: PL3078 Fossil Beach (P304427–8, P304437, P304415, ten specimens); Balcombe Bay (P308751–3, three specimens); Schnapper Point (P308755, two specimens); Braeside Tunnel (P30445, one specimen); Campbells Point (P304436, one specimen); PL3069 Red Bluff, Shelford (P304435, one specimen); Shelford (P304420, one specimen); Overburden, Batesford Limestone Quarry (P308811, P309021–3, P310316, P310313, six specimens).

Cadell Marl: PL3084 south of Morgan, South Australia (P304430, one specimen).

Bairnsdalian

Fyansford Formation: Grices Creek (P14594, P304425, five specimens); PL3103 downstream Grices Creek (P308754, one specimen); Grices Creek, middle beds (P304414, one specimen); PL3100 Murgheboluc 4A (P308735, one specimen).

Remarks. The holotype of *Cypraea consobrina* McCoy is a slightly immature, water-worn specimen found in the Moorabool River near Geelong, washed out of the Fyansford Formation. The posterior and anterior canals are not so highly callused, even when allowing for wear, as typical specimens of *Z. platypyga*. However, these forms intergrade and it is synonymised with the latter.

The holotype of *Cypraea toxorhyncha* Tate is a large specimen, with the extensions of the posterior canal very well developed. The anterior canal is very long and reflexed dorsally. Similar specimens are associated with and intergrade with typical *Z. platypyga* specimens in the Muddy Creek Formation and the Fyansford Formation. This name is also synonymised with *Zoila platypyga*. The holotype of *Zoila (Zoila) platypyga simplicior* Schilder, 1935, said to be in the Teale collection, Natural History Museum, London, cannot be located. Schilder indicated that it came from Muddy Creek and that it differed from *Z. platypyga* sensu stricto by having less produced and less rounded extremities,

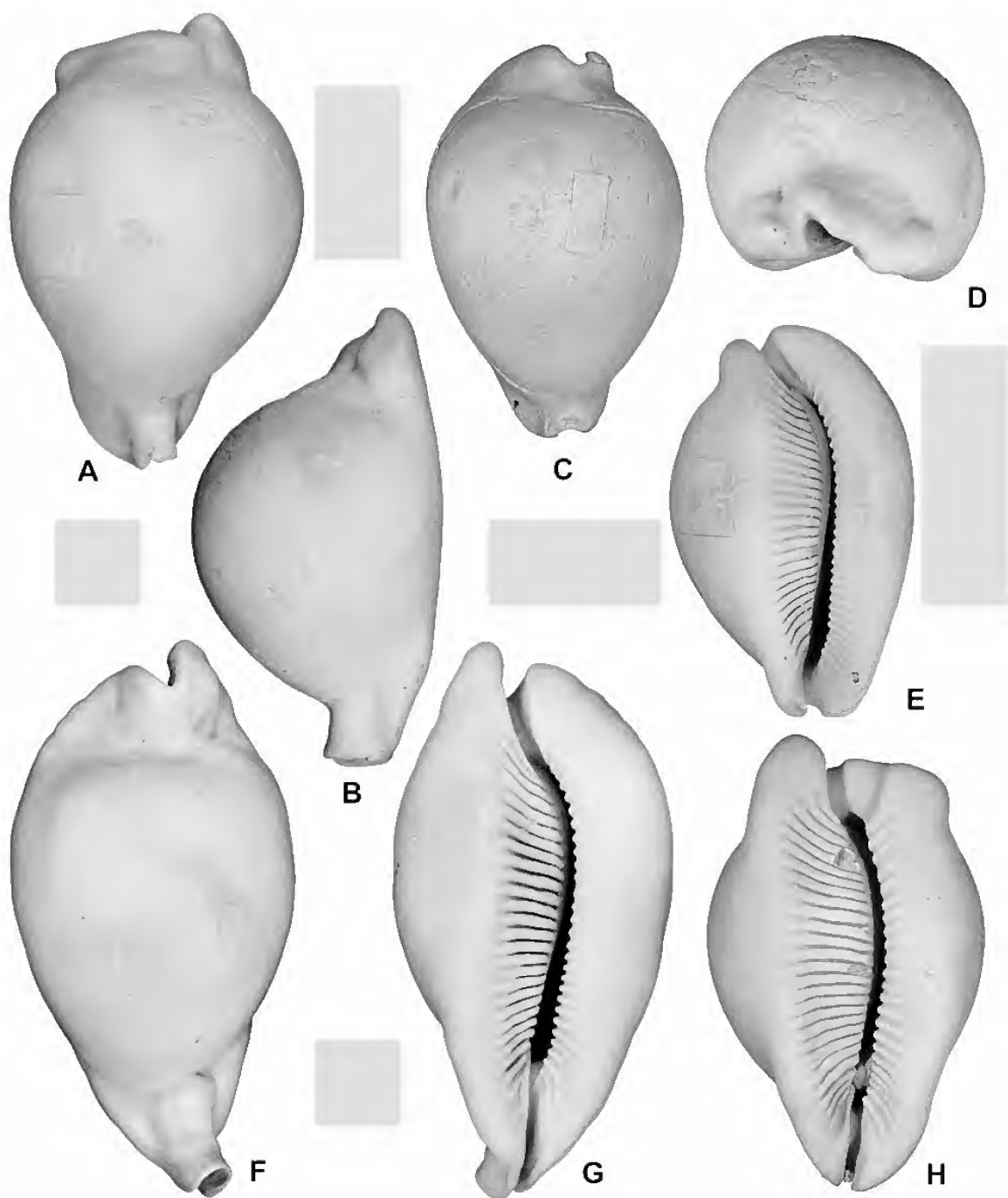


Figure 11. A–H, *Zoila platypyga*; A–B, D, H, holotype, P12137, Mount Eliza, $\times 1$; C, E, holotype of *Cypraea consobrina* McCoy, P12134, Mooroolbool River, $\times 1$; F–G, holotype of *Cypraea toxorhyncha* Tate, SAM T 823, Muddy Creek, $\times 1$.

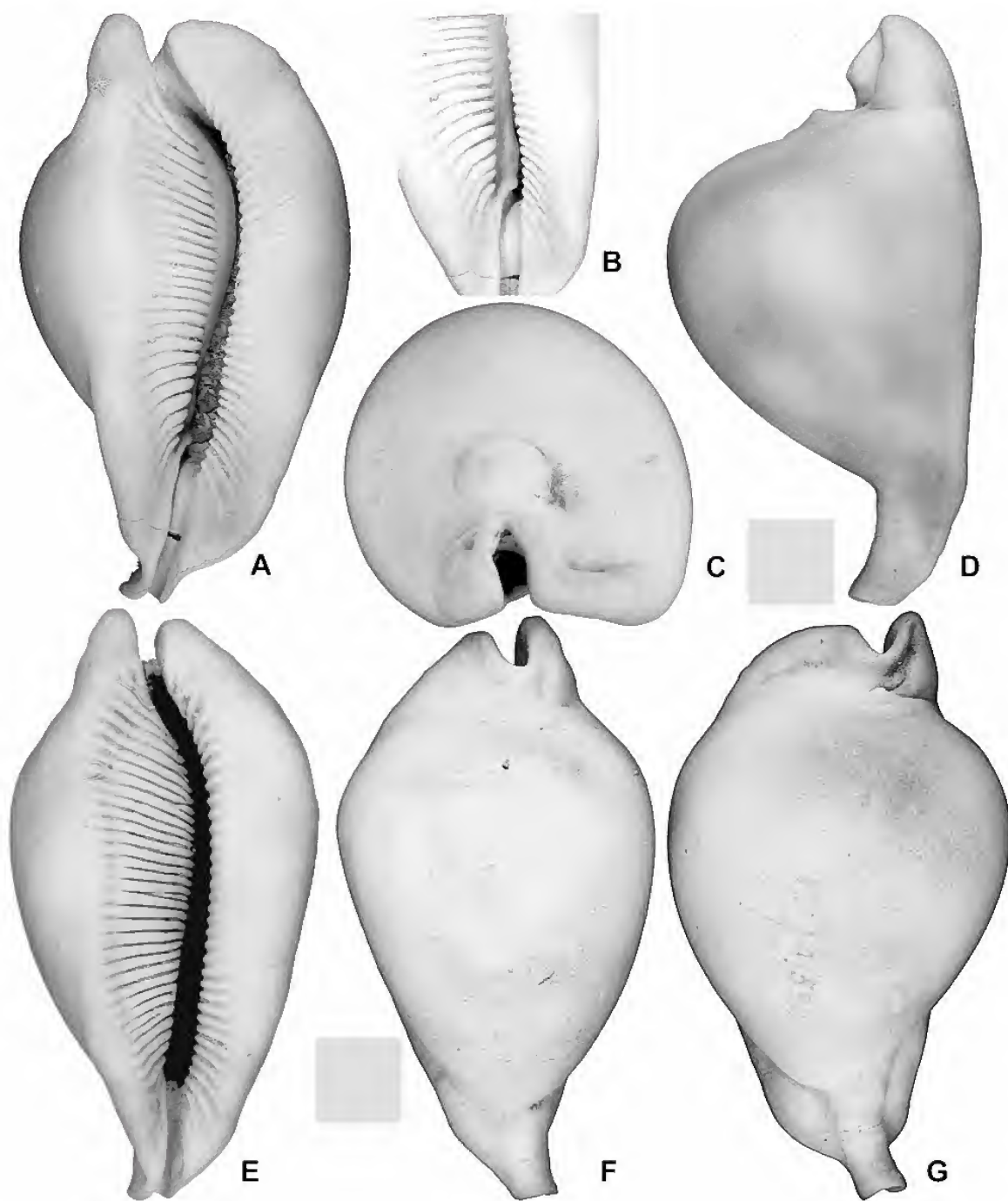


Figure 12. A–H, *Zoila platypyga*; A–D, G, P14594, Grices Creek, $\times 1$; E–F, P304414, Grices Creek, $\times 1$.

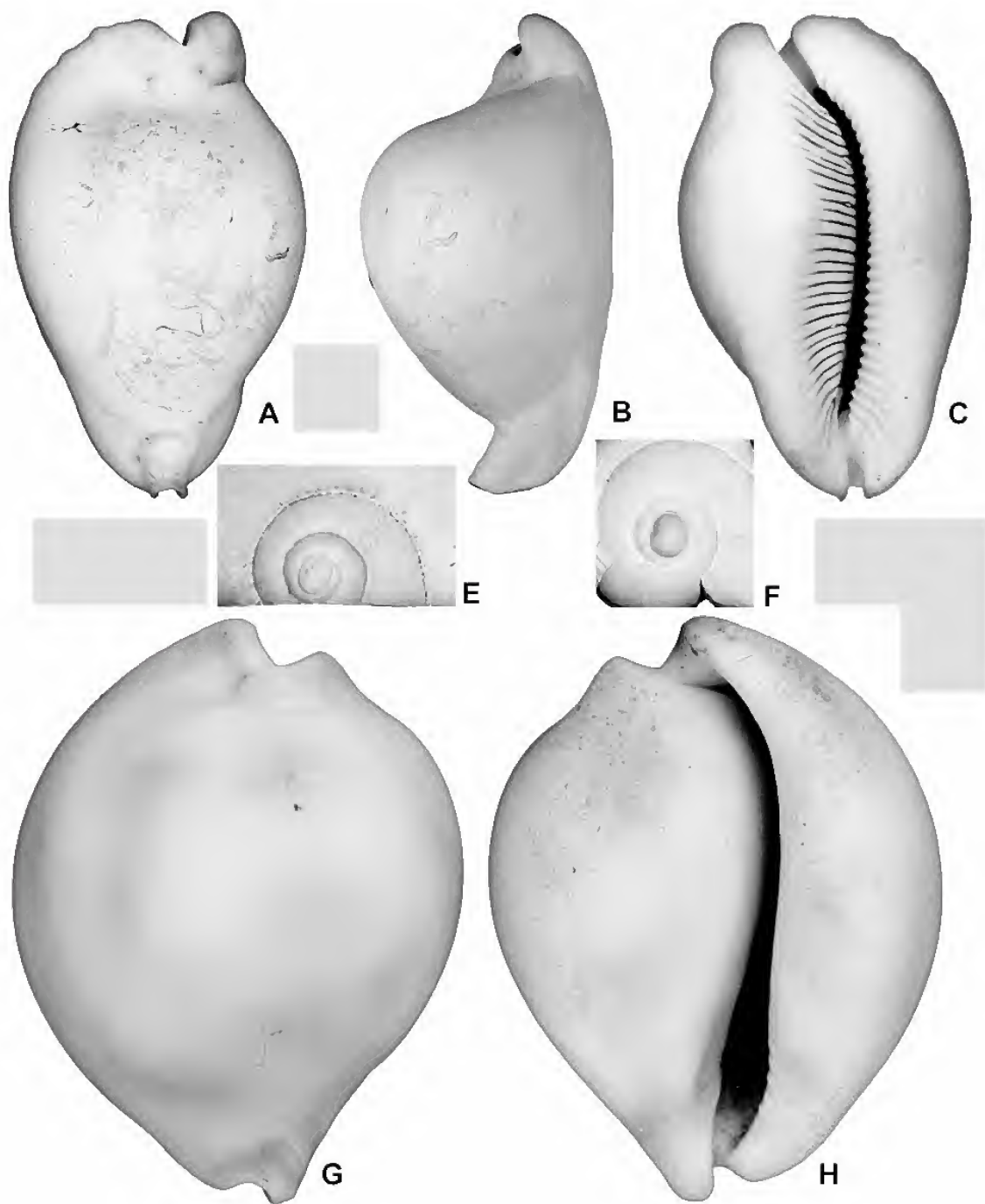


Figure 13. A–C, *Zoila platypyga*, P304415, PL 3078, $\times 1$; E–H, *Z. gigas*; E, protoconch, P308804, Muddy Creek, $\times 2.5$; F, protoconch, P308807, Batesford Quarry, $\times 2$; G–H, holotype of *Cypraea dorsata* Tate, SAM T849, Muddy Creek, $\times 1$.

less developed lateral flanges and a less projecting spire. The posterior extremity was bent to the left. These differences in callus development are minor intraspecific variations, as the specimens illustrated in figs. 11–13 show. Schilder stated that it bore a resemblance to *Z. consobrina* and that it came from a younger horizon than the latter. In fact, the holotype of *consobrina* comes from the same stratigraphical horizon.

Zoila gigas McCoy, 1867

Figures 2B, 13E–H, 14A–H, 15A–E

Cypraea gigas McCoy, 1867a:18.— McCoy, 1867b:194.— McCoy, 1867c:438.

Cypraea (Aricia) gigas McCoy.— McCoy, 1875:19, pl. 15; pl. 16, fig. 2; pls. 17–18, fig. 1; — McCoy, 1876, p. 35, pls. 28–29, fig. 1.

Cypraea dorsata Tate, 1890:212.— Tate, 1892, pl. 10, fig. 4; pl. 11, fig. 6.

Cypraea (Erosaria) gigas McCoy.— Harris, 1897:208.

Cypraea gabrieli Chapman, 1912:190, pl. 13, figs 1–3.

Gisortia gigas (McCoy).— Vredenburg, 1927:58.

Gisortia dorsata (Tate).— Vredenburg, 1927:58.

? *Gigantocypraea gigas* (McCoy).— Schilder, 1930:126, fig. 34–5 (cast).

Zoila (Gigantocypraea) gigas (McCoy).— Schilder, 1935:337, 338, fig. 17. — Wilson and Clarkson, 2004:53, pl. 57.

Zoila (Gigantocypraea) dorsata (Tate).— Schilder, 1935:337, 338.

Description. Shell solid, very large for genus, globose, covered with glaze, humped at dorsal midpoint of shell. Ventral surface flat to slightly concave on most specimens. Spire scarcely projecting, covered with thick callus. Four teleoconch whorls. Protoconch of two whorls, the first depressed, large, irregular, with finely granulated surface, coiled at an angle to axis of teleoconch whorls. Posterior canal bounded by very thick walls, deeply incised, strongly reflexed dorsally, deeply notched. Anterior canal short, about same length as posterior canal, narrow, deeply incised, strongly reflexed dorsally. Aperture very sinuous, widest at beginning of anterior canal; outer lip with 2–28 teeth, on most specimens only extending to midpoint of lip. Columellar lip edentulous. Fossula scarcely differentiated from columellar lip, relatively small, slightly depressed, somewhat rectangular, extending only slightly into aperture, bounded by very weak terminal ridge.

Dimensions.

	L	W	H	LT	CT
Lectotype P12139	212	143	109	8	—
SAM T849	99	76	65	7	— holotype <i>C. dorsata</i>
P12366	135	98	72	—	— holotype <i>C. gabrieli</i>
Figured specimen P13060	167	108	90	18	— Grices Creek
Figured specimen P308774	197	138	98	12	—
P308679	145	102	91		
P12969	247	174	126 largest specimen in collection.		

Type locality. ‘Blue clay of Muddy Creek, 10 miles south of Hamilton’, (i.e. PL3082 Clifton Bank, Muddy Creek, 7 km west of Hamilton, Victoria). AMG Coleraine WD 818225. Muddy Creek Formation. Balcombian, Middle Miocene.

Type material. Lectotype P12139, presented Lindsay Clarke. McCoy’s figured specimen chosen as lectotype.

Holotype of *Cypraea dorsata* Tate, SAM T849, Muddy Creek, Ralph Tate collection.

Holotype of *Cypraea gabrieli* Chapman, P12366, Bird Rock cliffs, presented by C.J. Gabriel, 3 April 1912.

Figured specimen P13060, presented W.H. Gregson 14 April 1919; figured specimen P308774, collected F.P. Spry 1922.

Time range. Janjukian–Bairnsdalian, Late Oligocene–Middle Miocene.

Occurrence and material. Janjukian. Jan Juc Formation: Bird Rock cliffs, Torquay (P308679, P308801, one specimen and one fragment); Deadmans Gully, Torquay (P315577, one specimen).

Batesfordian.

Gellibrand Formation: PL3047 cutting Princetown–Simpson Road (P308786, one fragment).

Balcombian

Muddy Creek Formation: Muddy Creek (P12969, P219370, P61265, P308774, P308794, P308780, P308772–3, 11 specimens); PL3082 Clifton Bank (P308776, P308795, two specimens).

Gellibrand Formation: Southeast of Gibson Beach (P54362, P308682, two specimens).

Fyansford Formation: PL3078 Fossil Beach (P308677, 308779 two specimens); Balcombe Bay (P308683–5, three specimens); Mornington (P308782, one specimen); Schnapper Point (P24866, P30777–8, three specimens); Port Phillip (P308781, one specimen); Altona Bay Coal Shaft (P308787, one fragment); Batesford (P308790, one specimen); Overburden, Batesford Quarry (P303315, one specimen and one fragment); Orphanage Hill (P308784, one specimen).

Morgan Limestone: Broken Cliffs opposite Waikerie, Murray River Cliffs, South Australia (private collection, Mannum).

Bairnsdalian

Gellibrand Formation: Glenample Steps (P308771, one specimen); Princetown (P5288, one specimen).

Fyansford Formation: Grices Creek (P5286, P12968, P12970, P13060, P308681, five specimens); Middle beds, Grices Creek (P308680, one specimen); Murgheboluc (P308678, one specimen).

Casts of a large cowry — which, due to their size, are almost certainly this species — have been found as follows:

Longfordian?

Gambier Limestone: Mount Gambier (P61262, one specimen, BM(NH) one specimen).

Batesfordian.

Curlew Limestone: Curlew (P308806, one specimen).

Balcombian

Nullarbor Limestone: 5 km south of Watson Station, South Australia (P316748, one specimen).

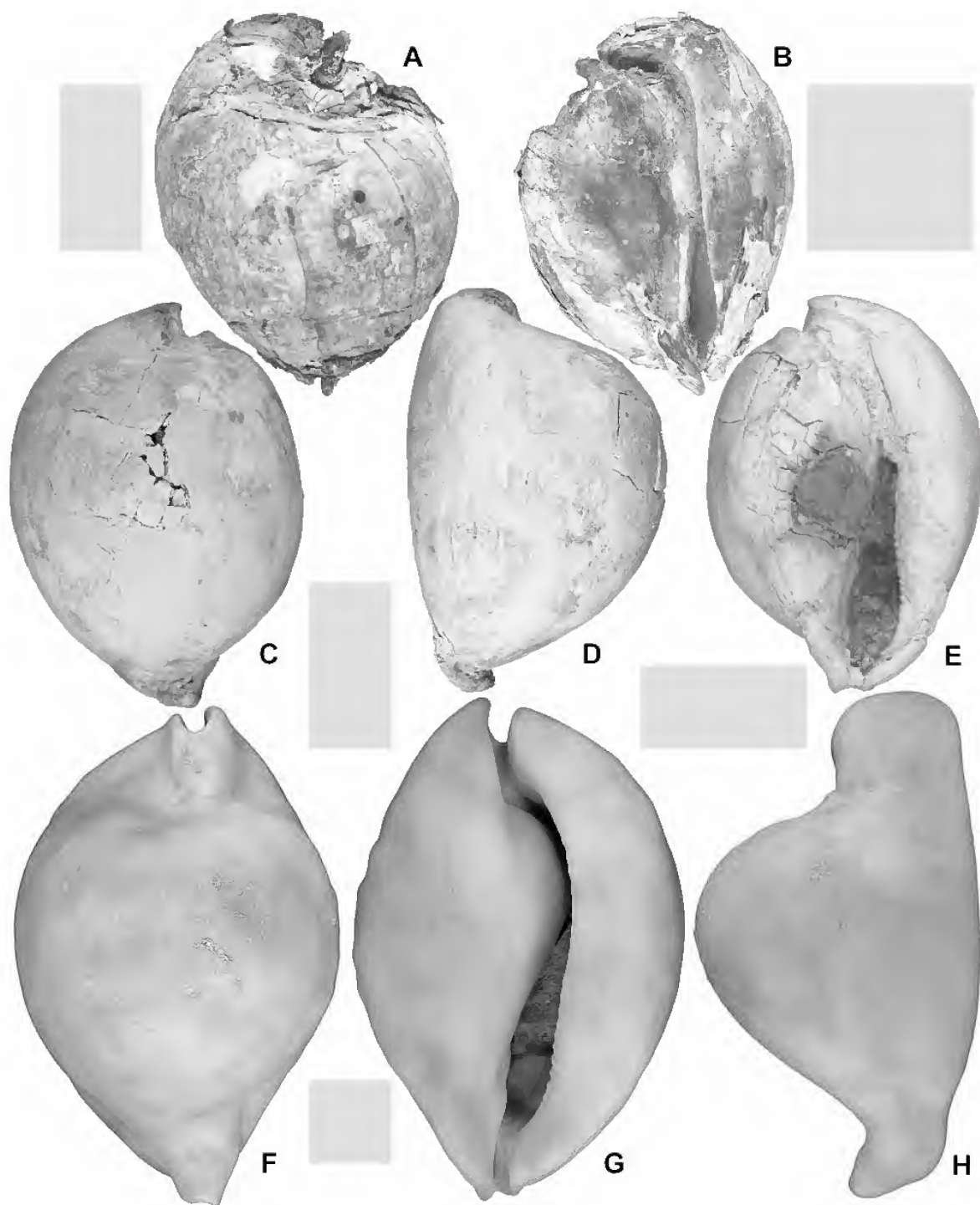


Figure 14. A–H, *Zoila gigas*; A–B, holotype of *Cypraea gabrieli* Chapman, P12366, Bird Rock cliffs, Torquay, $\times 0.5$; C–E, P308679, Bird Rock cliffs, $\times 0.5$; F–H, P13060, Grices Creek, 0.5.

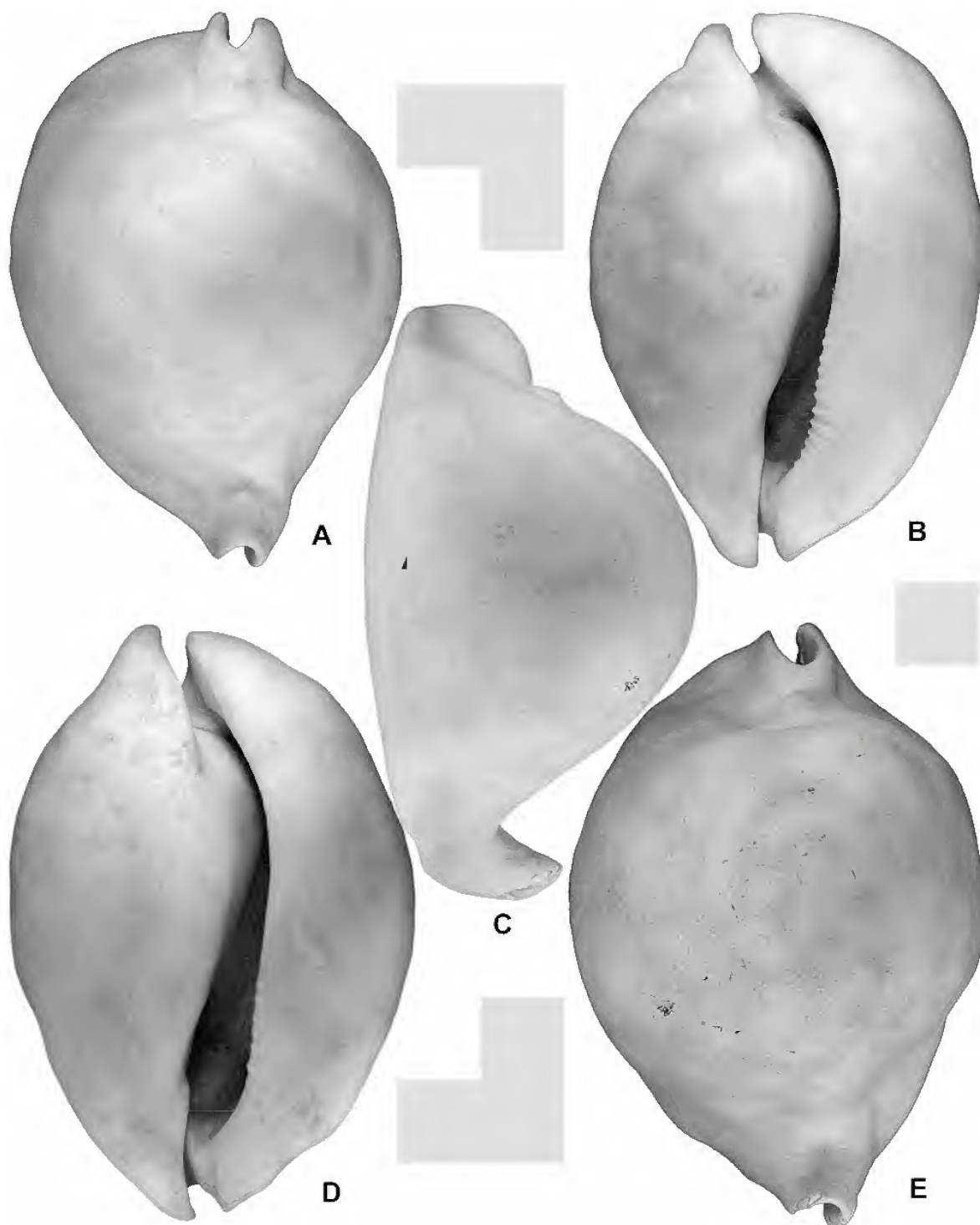


Figure 15. A–E, *Zoila gigas*; A–B, P308774, Clifton Bank, $\times 0.5$; C–E, lectotype, P12139, Muddy Creek, $\times 0.5$.

Fyansford Formation: Keilor (P58646, one specimen); sewerage excavation, Belmont (P308688, one specimen).

Gippsland Limestone: Newmerella Railway cutting (P308686, one specimen).

Morgan Limestone: Blanchetown (P316749, one specimen); 'Brittan', Murray River cliff 4.8 km downstream of Morgan (P316751, one specimen).

Remarks. This is the largest known Australian cowry, living or fossil. Specimens over 190 mm in length are not uncommon. Specimens are quite common in the middle Miocene, but because of their size, complete or undamaged specimens are uncommon. *Cypraea dorsata* Tate is merely a small specimen of *Zoila gigas*. The general shape, fossula and aperture are the same. The main difference is that the anterior and posterior canals are more strongly developed in most large specimens of *Z. gigas*. Small specimens, like the type of *C. dorsata*, occur with larger specimens at Fossil Beach, Grices Creek, Muddy Creek and Batesford Quarry, and there are also gradations between the smallest and the largest specimens. For these reasons, *C. dorsata* is synonymised with *Z. gigas*.

Cypraea gabrieli Chapman was based on a crushed specimen from the Jan Juc Formation, which is very difficult to compare with other material. The main differences between it and the lectotype of *Z. gigas* McCoy are a depressed spire, the lack of callus covering the spire and the presence of a dimpled dorsum. Only one other specimen from the Jan Juc Formation is available. This is complete and uncrushed, but has a very chalky shell. There are well-developed teeth on the outer lip extending to about midway on the lip. On the columella there are some very low but distinct teeth situated over the fossula and about midway along the aperture. The dorsum is smooth and the base is rounded rather than flat or convex. Apart from the presence of the columellar teeth, this specimen closely matches a similar-sized specimen from the Fyansford Formation at Grices Creek in all features including the spire and fossula. McCoy pointed out there were weak teeth just visible on the columella of the holotype of *Z. gigas*. The significance, if any, of the presence of the dimpled dorsum cannot be assessed as there are so few specimens. Because there are no consistent differences between the two specimens from the Jan Juc Formation and specimens of *Z. gigas* from the Fyansford Formation, *Cypraea gabrieli* is regarded as a further synonym of *Z. gigas*.

The protoconch of this species (figs 2B, 13E–F) is different from those of other species of *Zoila* and also from those of species of *Umbilia*. There are fewer whorls and the first is irregular in shape, suggesting that it might originally have been chitinous and subsequently calcified. Other species of *Zoila* are similar to species of *Umbilia* in that they have a smooth, regular protoconch of three whorls, and a coiling axis at an angle to that of the teleoconch.

Zoila sp.

Figures 16C–D, M

Zoila sp. McNamara and Kendrick, 1994:34.

Description. Shell solid, small for genus, somewhat globose. Spire covered with callus, not projecting. Posterior canal short,

notched. Anterior canal missing; slight trace of anterior basal extension on left flank. Aperture narrow, very slightly curved; outer lip with well-developed, elongate teeth (15 teeth preserved). Columellar lip with well-developed teeth extending along the whole aperture (18 teeth preserved). Base of shell rounded on both sides of aperture. Fossula well developed, concave, broad and spoon-shaped, bounded anteriorly by well-developed, single terminal ridge.

Dimensions.

	L	W	H
Figured specimen WAM 82.549	48+	36	30

Figured material. WAM 82.549, collected K. J. McNamara and G. W. Kendrick, September 1981.

Occurrence. Locality 12, Latitude Point, from large boulders of pink limestone fallen from upper level of cliff, Barrow Island, Western Australia. Poivre Formation, middle Miocene.

Remarks. This species is known only from a single specimen, which has a small piece of the left side of the posterior canal broken off, as well as a large portion of the right side of the anterior end, including the posterior canal. As a consequence, detailed comparison with other species is not possible; however, there is enough of the specimen preserved to indicate that it is a species of *Zoila* and almost certainly ancestral to the younger species occurring in Western Australia. Both aperture and fossula are very similar to those of *Z. campestris* sp. nov. from the late Pliocene, Roe Calcarenite. It differs from *Z. campestris* in that its outline is more rounded and it does not have a flat base. The dorsum is also not humped anteriorly as in *Z. campestris* sp. nov. It bears no close resemblance to any of the fossil species known from southeast Australia.

Zoila sp. is somewhat similar to the middle Pliocene species *Zoila gendingensis* (Martin, 1899) from the Upper Kalibeng Formation of Sonde, Java, Indonesia, but is not so high and does not have the flat base of that species. The dorsum is not as humped as in *Zoila kendengensis* Schilder, 1941 from the Pleistocene Putiangan Formation of Java and neither does it have the flat base of that species. Of the living species of the genus, it is most similar to *Zoila venusta* (Sowerby, 1846), known from the Great Australian Bight to Shark Bay, Western Australia.

Zoila campestris sp. nov.

Figures 16A–B, E–J, O

Cypraea (Zoila) sp. Ludbrook, 1978, p. 129, pl. 13, fig. 19.

Zoila sp. Wilson and Clarkson, 2004: 52, pl. 55, figs a, b.

Description. Shell solid, polished, of average size for genus, globose, surface on some specimens malleated with rectangular depressions, with sides about 1.5 mm long; ventral surface flattened. Spire barely protruding beyond last whorl, covered with thick callus. Posterior canal short, notched, sides thickened. Anterior canal very short, abruptly truncated, deeply incised. Aperture sinuous, widened above fossula; outer lip with 17–24 well-developed teeth, extending along entire lip;

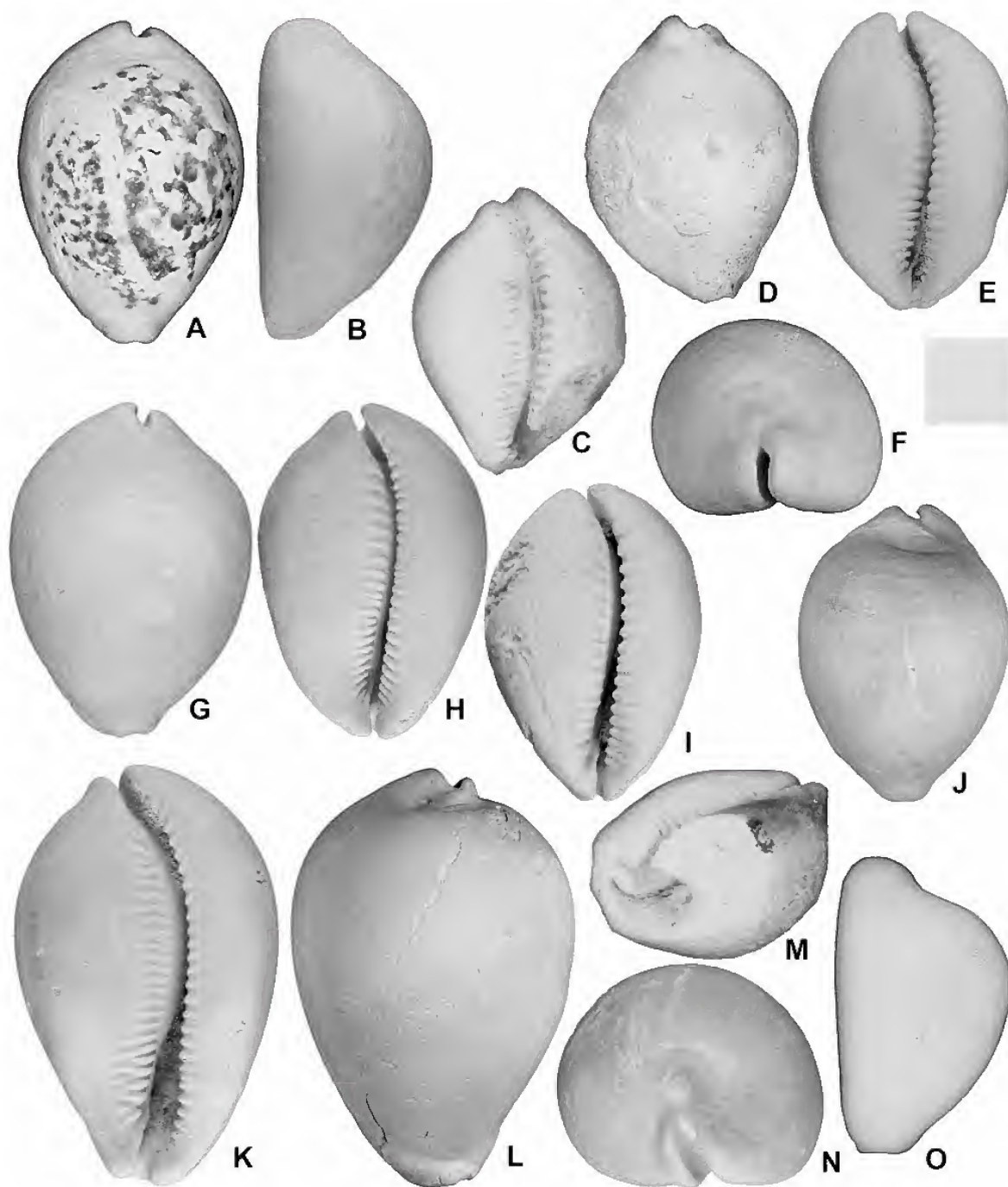


Figure 16. A–B, E–J, O, *Zoila campestris*; A–B, paratype, WAM 89.437, Roe Plain, Western Australia, uncoated to show colour pattern, $\times 1$; E, J, O, paratype, P308704, Roe Plain, $\times 1$; F–H, holotype, WAM 89.177, Roe Plain, $\times 1$; C–D, M, *Z. sp.*, WAM 82.549, Barrow Island, Western Australia, $\times 1$; K–L, N, *Z. fodinata*, holotype, WAM 89.637, Roe Plain, Western Australia, $\times 1$.

inner lip with 17–21 well-developed teeth, extending along entire lip. Fossula well developed, deeply depressed, bounded anteriorly by sharp terminal ridge. Colour pattern present on some specimens, of brown ground with darker brown patches.

Dimensions.

	L	W	H	LT	CT
Holotype WAM 89.177	57	41	34	27	21
Paratype WAM 89.437	55	38	30	18	18
Paratype NMV P308704	51	36	30	20	19

Type locality. Quarry 2.5 km north of Hampton microwave repeater tower, Roe Plains, Western Australia. AMG Eucla 1:250,000 sheet CK365465. Roe Calcarenite.

Type material. Holotype WAM 89.177, collected G.W. Kendrick 27–30 October 1988; paratype WAM 89.437, collected Sam Rowe, January 1989; paratype NMV P308704, collected T. A. Darragh, 9 August 1973.

Time range. Pliocene.

Occurrence and material. Roe Calcarenite: PL3172 Hampton Tower (P308704-5, WAM 69.494, 70.17, six specimens); PL3167 1.5 km north of Hampton Tower (P308703, WAM 80.109, three specimens); PL3166 2.5 km north of Hampton Tower (P121293, WAM 89.178, 89.437, 89.637, four specimens).

Remarks. At first glance, small specimens of this species may be confused with the common *Austrocypraea amae* Fehse and Kendrick of the Roe Calcarenite, but they are readily distinguished by their smooth fossula. In *Austrocypraea*, the columellar teeth are produced into thin ribs that continue across the fossula. This species is most closely related to the living species *Zoila decipiens* (Smith, 1880), Recent, Western Australia, from which it differs by having stronger teeth and teeth present along the entire columella. It is also globose in shape rather than pyriform as in *Z. decipiens* and lacks the prominent protruding spire of that species. The fossula is very similar to that of the *Z. decipiens*. It is not closely similar to the fossil species of *Zoila* known from the Oligocene and Miocene of southeast Australia, with the exception of a species known from a single broken specimen from the upper Miocene of Victoria. *Z. campestris* bears some resemblance to *Zoila kendengensis* Schilder, 1941 from the Pleistocene Putiangan Formation of Java, but that species has relatively prominent anterior and posterior canals.

Etymology. Latin *campester*, pertaining to a plain.

Zoila fodinata sp. nov.

Figures 16K–L, N

Description. Shell solid, polished, of average size for the genus, globose, pyriform, ventral surface rounded. Spire slightly protruding beyond last whorl, covered with thick callus. Posterior canal short, notched, sides thickened. Anterior canal very short, abruptly truncated, deeply incised. Aperture sinuous, widened above fossula; outer lip with 25–28 well-developed teeth, extending along entire lip; inner lip with 21–

25 well-developed teeth, extending along entire lip. Fossula well developed, subrectangular, concave, bounded on inner side by low ridge and anteriorly by sharp terminal ridge; terminal ridge rather broad, extending down into aperture as sharp ridge forming anterior edge of fossula.

Dimensions.

	L	W	H	LT	CT
Holotype WAM 89.637	72	47	39	28	24

Type locality. Quarry 2.5 km north of Hampton microwave repeater tower, Roe Plains, Western Australia. AMG Eucla 1:250,000 sheet CK365465. Roe Calcarenite.

Type material. Holotype, WAM89.637, collected G.W. Kendrick, 27–30 October 1988.

Time range. Pliocene

Occurrence and material. Roe Calcarenite: PL3166 2.5 km north of Hampton Tower (one specimen).

Remarks. This species is most closely similar to the living species *Zoila venusta*, from which it differs by having stronger teeth and teeth present along the entire columella. The fossula is also shallower but deeper within the aperture than in *Z. venusta*. It is not as globose, being more pyriform. It does not seem to be closely similar to the fossil species of *Zoila* known from the Oligocene and Miocene of southeast Australia.

Etymology. Latin, *fodina*, a quarry.

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References

- Beu, A. G. and Darragh, T. A. 2001. Revision of southern Australian Cenozoic fossil Pectinidae (Mollusca, Bivalvia). *Proceedings of the Royal Society of Victoria* 113(1): 1–205.
- Bouchet, P. and Rocroi, J.-P. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47(1-2): 1–397.
- Cernohorsky, W. O. 1971. Fossil and Recent Cypraeaacea (Mollusca: Gastropoda) of New Zealand with descriptions of new species.

- Records of the Auckland Institute and Museum* 8: 103–129.
- Chapman, F. 1912. New or little-known Victorian fossils in the National Museum. Part XV. Some Tertiary Gastropoda. *Proceedings of the Royal Society of Victoria* 25(1): 186–192, pls. 12–13.
- Conrad, T. 1848. Observations on the Eocene formation, and descriptions of one hundred and five new fossils of that period, from the vicinity of Vicksburg, Mississippi, with an Appendix. *Proceedings of the Academy of Natural Sciences of Philadelphia* 3(11): 280–299.
- Conrad, T. 1865. Catalogue of the Eocene and Oligocene Testacea of the United States. *American Journal of Conchology* 1(1): 1–35.
- Cossmann, M. 1903. *Essais de Paléoconchologie comparée* Author, Paris, vol. 5, 215 pp., 9 pls.
- Cox, L. R. 1930. The fossil fauna of the Samana Range and some neighbouring areas: Part VIII. The Mollusca of the Hangu Shales. *Memoirs of the Geological Survey of India*, new series, 15: 129–222, pls. 17–22.
- Dall, W. H. 1890. Contributions to the Tertiary fauna of Florida. *Scientific Transactions of the Wagner Free Institute of Philadelphia* 3(1): 1–200, pls. 1–12.
- Darragh, T. A. 2002. A revision of the Australian genus *Umbilia* (Gastropoda: Cypraeidae). *Memoirs of the Museum Victoria* 59(2): 355–392.
- Deshayes, G. P. 1835 [1824–1837]. *Description des coquilles fossiles des environs de Paris*, 2: 2–814, Paris, Author.
- Dolin, L. 1991. Cypraeoidea and Lamellarioidea (Mollusca: Gastropoda), from the Chipola Formation (late Early Miocene) of northwestern Florida. *Tulane Studies in Geology and Paleontology* 24: 1–60.
- Dolin, C. and Dolin, L. 1983. Révision des Triviacea et Cypraeacea (Mollusca, Prosobranchia) éocènes récoltés dans les localités de Gan (Tuilerie et Acot) et Bosdarros (Pyrénées-Atlantiques, France). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geology* 20(1): 5–48.
- Edwards, F. E., 1854 [1849–1877]. *A monograph of the Eocene Mollusca, or descriptions of shells from the older Tertiaries of England*. Palaeontographical Society, London.
- Gaskoin, J.S. 1849. Descriptions of new species of the genus *Cypraea*. *Proceedings of the Zoological Society of London* 16: 90–8.
- Grateloup, J. P. S. 1827. Descriptions de plusieurs espèces de coquilles fossiles des environs de Dax (Landes). *Bulletin d'Histoire Naturelle de la Société Linnéenne de Bordeaux* 2(7): 3–26.
- Groves, L. T. 1990. New species of Late Cretaceous Cypraeacea (Mollusca: Gastropoda) from California and Mississippi, and a review of Cretaceous cypraeaceans of North America. *Veliger* 33(3): 272–285.
- Groves, L. T. 2004. New species of Late Cretaceous Cypraeidae (Gastropoda) from California and British Columbia and new records from the Pacific slope. *The Nautilus* 118(1): 43–51.
- Harris, G. F. 1897. *Catalogue of Tertiary Mollusca in the Department of Geology, British Museum (Natural History). Part 1. The Australasian Tertiary Mollusca*. British Museum (Natural History), London, 407 pp., 8 pls.
- Iredale, T. 1935. Australian Cowries. *The Australian Zoologist* 8(2): 96–135, pls. 8–9.
- Johnston, R.M. 1888. *Systematic account of the geology of Tasmania*. Government Printer, Hobart, 408 pp., 66 pls.
- Jousseaume, F. 1884a (15 February). Division des Cypraeidae. *Le Naturaliste* 6(52): 414–415.
- Jousseaume, F. 1884b. Étude sur la Famille des Cypraeidae. *Bulletin de la Société Zoologique de France* 9: 81–100.
- Kay, E. A. 1990. Cypraeidae of the Indo-Pacific: Cenozoic fossil history and biogeography. *Bulletin of Marine Science* 47(1): 23–34.
- Liltved, W.R. 1989. *Cowries and their relatives of Southern Africa*. Seacomber Publications, Cape Town, 208 pp.
- Ludbrook, N.H. 1978. Quaternary molluscs of the western part of the Eucla Basin. *Geological Survey of Western Australia Bulletin* 125, 286 pp.
- MacNeil, F.S. and Dockery, D.T. 1984. Lower Oligocene Gastropoda, Scaphopoda, and Cephalopoda of the Vicksburg Group in Mississippi. *Mississippi Bureau of Geology Bulletin* 124, 415 pp.
- McCoy, F. 1867a. On the Recent zoology and palaeontology of Victoria. *Intercolonial Exhibition Essays, 1866–67*, Melbourne, 24 pp.
- McCoy, F. 1867b. On the Recent zoology and palaeontology of Victoria. *Annals and Magazine of Natural History* series 3, 20: 175–202.
- McCoy, F. 1867c. Description of two new fossil cowries characteristic of Tertiary beds near Melbourne. *Annals and Magazine of Natural History* series 3, 20: 436–438.
- McCoy, F. 1875. *Prodromus of the Palaeontology of Victoria*, decade 2: 1–37, pls. 11–20, Melbourne.
- McCoy, F. 1876. *Prodromus of the Palaeontology of Victoria*, decade 3: 1–40, pls. 21–30, Melbourne.
- McCoy, F. 1877. *Prodromus of the Palaeontology of Victoria*, decade 5: 1–41, pls. 41–50, Melbourne.
- McNamara, K. J. and Kendrick, G. W. 1994. Cenozoic Molluscs and Echinoids of Barrow Island, Western Australia. *Records of the Western Australian Museum Supplement* 51, 50 pp.
- Meyer, C. P. 2003. Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* 79:401–459.
- Meyer, C. P. 2004. Toward comprehensiveness: increased molecular sampling within Cypraeidae and its phylogenetic implications. *Malacologia* 46: 127–156.
- Mulder, J. F. 1897. What geology teaches. *Geelong Naturalist* 6(2): 21–24.
- Petuch, E. J. 2004. *Cenozoic seas. The view from Eastern North America*. CRC Press, Boca Raton, 328 pp.
- Pritchard, G. B. 1896. A revision of the fossil fauna of the Table Cape beds, Tasmania, with descriptions of the new species. *Proceedings of the Royal Society of Victoria* 8: 74–150, pls. 2–4.
- Ranson, G. 1967. Les protoconques ou coquilles larvaires des Cyprées. *Mémoires du Muséum national d'Histoire naturelle, Séries A*, 47(2): 93–126, pls. 1–39.
- Schilder, F. A. 1926. Additions and corrections to Vredenburg's classification of the Cypraeidae. *Records of the Geological Survey of India* 58(4): 358–379.
- Schilder, F. A. 1927. Revision der Cypraeacea (Moll., Gastr.). *Archiv für Naturgeschichte* A, 91: 1–165.
- Schilder, F. A. 1930. The Gisortidae of the world. *Proceedings of the Malacological Society of London* 19: 118–138, pls. 11–12.
- Schilder, F. A. 1932. Cypraeacea. *Fossilium Catalogus*. 1: Animalia 55: 1–276.
- Schilder, F. A. 1935. Revision of the Tertiary Cypraeacea of Australia and Tasmania. *Proceedings of the Malacological Society of London* 21: 325–355.
- Schilder, F. A. 1939. Die Genera der Cypraeacea. *Archiv für Molluskenkunde* 71(5–6): 165–201.
- Schilder, F.A. 1941. The marine Mollusca of the Kendeng Beds (East Java). Gastropoda, Part III (Families Eratoidea, Cypraeidae, and Amphiperatidae). *Leidsche Geologische Mededeelingen* 12: 171–194.
- Schilder, F. A. and Schilder, M. 1939. Prodrôme of a monograph on living Cypraeidae. *Proceedings of the Malacological Society of London* 23: 119–231.

- Smith, E.A. 1880. Description of twelve new species of shells. *Proceedings of the Zoological Society of London* 48: 478-485, pl., 48.
- Sowerby, G. B. (II) 1846. Description of a new cowry. *Proceedings of the Linnean Society of London* 1: 314.
- Tate, R. 1890. The gastropods of the Older Tertiary of Australia. (Part III). *Transactions of the Royal Society of South Australia* 13: 185-235.
- Tate, R. 1892. Nine plates illustrative of Professor Tate's paper on the gastropoda of the Tertiary of Australia — Part 3 in Volume 13 of the Society's Transactions. *Transactions of the Royal Society of South Australia* 15: pls. 5-13.
- Tate, R. 1893. The gastropods of the Older Tertiary of Australia. Part IV. (including supplement to Part III). *Transactions of the Royal Society of South Australia* 17: 316-345, pls. 6-10.
- Thiele, J. 1929. *Handbuch der systematischen Weichtierkunde*, Fischer, Jena. vol. 1(1): 1-376.
- Tomida, S. 1989. Fossil molluscan assemblage from the Neogene Senhata Formation around Nokogiriyama, Boso Peninsula, Japan. *Bulletin of the Miunami Fossil Museum* 16: 85-108, pls. 10-19.
- Vredenburg, E. 1927. A review of the genus *Gisortia* with descriptions of several species. *Palaeontologica Indica* (n.s.) 7(3): 1-78, pls. 1-32.
- Wenz, W. 1941 (1938-44). Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. *Handbuch der Paläozoologie* 6(5): 949-1200.
- Wilson, B.R. 1985. Direct development in southern Australian cowries (Gastropoda: Cypraeidae). *Australian Journal of Marine and Freshwater Research* 36: 267-280.
- Wilson, B.R. 1993. *Australian Marine Shells*, vol. 1. Odyssey Publishing, Perth, 408 pp.
- Wilson, B.R. 1998. Superfamily Cypraeoidea. In: Beesley, P. L. et al. (eds), *Mollusca: The Southern Synthesis. Fauna of Australia*. CSIRO Publishing, Collingwood. 5B: 780-786.
- Wilson, B.R. and Clarkson, P. 2004. *Australia's spectacular cowries: a review and field study of two endemic genera: Zoila and Umbilia*. Odyssey Publishing, El Cajon, 396 pp.
- Wilson, B. R. and McComb, J. A. 1967. The genus *Cypraea* (subgenus *Zoila* Jousseaume). *Indo-Pacific Mollusca* 1(8): 457-484.
- Yates, A. M. 2009. The oldest South Australian cowries (Gastropoda: Cypraeidae) from the Paleogene of the St Vincent Basin. *Alcheringa* 33(1): 23-31.

A new species of *Peribrissus* (Echinoidea, Spatangoida) from the middle Miocene of South Australia

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Abstract

Holmes, F. C. 2011. A new species of *Peribrissus* (Echinoidea, Spatangoida) from the middle Miocene of South Australia. *Memoirs of Museum Victoria* 68: 29–35.

A new species of spatangoid echinoid from the middle Miocene Glenforslan Formation cropping out in the Murray River cliffs near Blanchetown, South Australia, is described and assigned to the genus *Peribrissus*. *Peribrissus janiceae* sp. nov. is only the third species of this genus to be recorded, and the first to occur outside the Mediterranean area of Europe and North Africa. Brief references are made to the similarity of certain features in *Prenaster*, *Pericosmus* and *Peribrissus*, which have caused confusion with identification in the past.

Keywords

Echinoidea, Spatangoida, *Peribrissus*, new taxa, middle Miocene, South Australia

Introduction

In the Miocene stratigraphic sequences along the Murray River and elsewhere in Australia, species belonging to the Spatangoida constitute approximately 50 per cent of the recorded taxa of irregular echinoids (Holmes et al., 2005). The discovery of yet another new species of spatangoid, albeit a single specimen, should come as no surprise considering the vast extent of these generally poorly examined outcrops in South Australia. However, what is intriguing is that the new species belongs to a genus that, so far, has been recorded in the literature from only the Mediterranean area of Europe and North Africa. The specimen was found by Chris Ah Yee and Janice Krause in 2007 at Museum Victoria locality PL3203 (see fig.1), the same location as the three specimens of *Murraypneustes biannulatus* Holmes et al., 2005, discovered in 2003.

Materials and methods

The specimen number prefixed ‘P’, on which this study is based, is housed in the Invertebrate Palaeontology Collection, Museum Victoria (NMV). Wherever possible, measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL), test width (%TW) or test height (%TH).

Age and stratigraphy

The Glenforslan Formation, in which the specimen was found, is synonymous with the Lower Morgan limestone, which conformably overlies the Finniss Formation and is of early middle Miocene (Batesfordian, Langian) age. The thickness of

the unit is relatively consistent at 13–15 m, although this is reduced in southern exposures due to post-middle Miocene uplift and subsequent erosion. Echinoids tend to be found at or above the floatstone–rudstone contact at the base of cycles composed of mollusc–bryozoan floatstone grading upward into *Celleporaria* rudstone tops (Lukasik and James, 1998). Sediments are pervasively mottled, obscuring all physical sedimentary textures. The middle Glenforslan Formation is interpreted as being deposited in relatively shallow waters, possibly less than 10 m, based on the presence of calcareous algae and mixotrophic foraminifers (Dr Jeff Lukasik, Petro-Canada Oil and Gas, Calgary, pers. com., 2005). This section of the formation forms part of the richest warm-water biotic record from southern Australia at a time of maximum transgression of the sea across the continental shelf (McGowran and Li, 1994, and papers cited therein).

Associated fauna

Refer to Holmes et al. (2005) for a table of echinoid species recorded from the Glenforslan Formation.

Systematic palaeontology

Order Spatangoida L. Agassiz, 1840

Suborder Paleopneustina Markov and Solov’ev, 2001

Family Prenasteridae Lambert, 1905

Remarks. The family Paleopneustidae A. Agassiz, 1904, together with the families Pericosmidae, Schizasteridae and Prenasteridae, initially established as tribes within the family

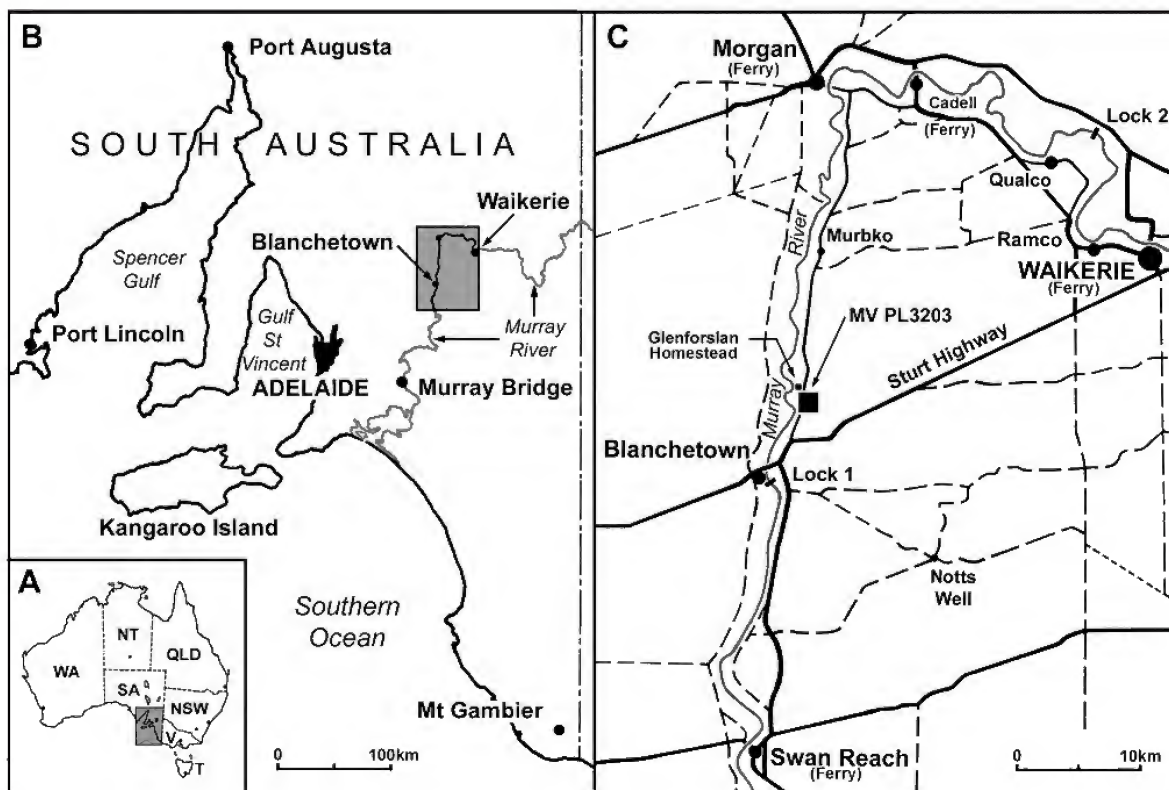


Figure 1. A and B, general location maps; C, map of Murray River between Waikerie and Swan Reach, South Australia, showing locality of NMV PL3203, north of Blanchetown.

Brissidae by Lambert (1905, p. 153), allowed numerous spatangoid genera to be divided into groups based primarily on the distinctive path followed by their fascioles. Lambert and Thiéry (1925, pp. 514–515) listed *Peribrissus* Pomel, 1883 as a subgenus of *Prenaster* Desor, 1853 within the tribe Prenasterinae. However, in subsequent classifications of the Order Spatangoida by Mortensen (1951), Termier and Termier (1953), Durham and Melville (1957), Fischer (1966) and Smith (1984), the family Prenasteridae was not recognised, and *Peribrissus* and *Prenaster* were placed within the Schizasteridae. Not until Smith et al. (2005) and Smith and Stockley (2005) did the family Prenasteridae reappear in any subdivision of the Spatangoida. Finally, Kroh and Smith (2010) presented a primary framework for the classification of post-Palaeozoic echinoids based on extant taxa into which fossil taxa have been incorporated. In this classification, Prenasteridae, Schizasteridae and Periasteridae form the Suborder Paleopneustina.

Genus *Peribrissus* Pomel, 1869

Type species. *Peribrissus sahelensis* Pomel, 1883, by subsequent monotypy.

Other species. *P. sotgiai* Giorgio, 1923.

Diagnosis. Modified from Smith et al. (2005). Test medium to large and cordiform with distinct anterior sulcus, posterior face oblique to vertically truncate, profile depressed to moderately domed. Apical disk well anterior of centre, ethmolytic with three gonopores. Ambulacrum III sunken aborally, the groove increasing in width and depth to ambitus, with rows of enlarged tubercles occurring just outside adradial sutures, pores small. Petals straight, narrow and depressed, cruciform, the anterior pair longer than the posterior pair. Peristome and plastron plating of type species unknown. Periproct high on posterior truncate face. Semipetalous fasciole band combines with continuous marginal fasciole immediately behind and below anterior petals.

Remarks. There has been confusion regarding the designation of the type species of *Peribrissus*. Fischer (1966, p. U576) and Smith et al. (2005) stated that *P. sahelensis* is the type species by original designation, but Pomel (1869, p. 13) did not name any species he assigned to his genus, for which he gave only a very brief diagnosis and made comparisons with *Prenaster*. Pomel later (1883, p. 36) gave a slightly more detailed diagnosis followed by the statement '*P. sahelensis* est du miocène supérieur'. As *sahelensis* was the only named species assigned

to *Peribrissus*, the diagnosis given for the genus applies also to the species, thus satisfying the criteria for availability (ICZN, Article 12.2.6) and making *P. sahelensis* the type species by subsequent monotypy (ICZN, Article 68.3).

Two species of *Pericosmus* described by McNamara and Philip (1964) from the Miocene of Australia — *P. celsus* and *P. quasimodo* — were reassigned by Smith et al. (2005) to *Peribrissus*. Though *Pericosmus* and *Peribrissus* are superficially alike, the path of the peripetalous fasciole in the two Australian species is clearly different from that in the *Prenasteridae* and, consequently, in *Peribrissus*. Smith et al. (2005) stated that in the *Prenasteridae*, ‘marginal and peripetalous fasciole combine anteriorly, the combined band passing several plates below the end of the anterior petals’. In contrast, the peripetalous fasciole in *Pericosmus celsus* and *P. quasimodo* — as well as in *P. torus*, also erected by McNamara and Philip in the same paper — follow a distinctly different path. These three species have the peripetalous fasciole closely bounding the distal end of the anterior petals, then transversely crossing interambulacral plates in columns 2a and 3b before taking a longitudinal path (sometimes irregular and/or intermittent) towards the marginal fasciole in interambulacral columns 2b and 3a. Due to the state of preservation of the numerous *Pericosmus* specimens inspected in Museum Victoria and private collections, it is not possible to determine whether the peripetalous fasciole always reaches the marginal fasciole on either side of the anterior sulcus. Nevertheless, in all Australian species assigned to *Pericosmus*, including *P. compressus* Duncan, 1877 and *P. maccoyi* Gregory, 1890, the peripetalous fasciole closely bounds the distal end of the anterior petals and continues transversely onto interambulacra 2 and 3, clearly negating any reassignment to *Peribrissus*. However, whether the five Australian fossil species listed above strictly belong in the genus *Pericosmus* is a matter of conjecture, considering the type species *Pericosmus latus* Desor in Agassiz and Desor, 1847, has separate and continuous marginal and peripetalous fascioles, the latter crossing ambulacrum III well above the anterior margin.

Stefanini (1911, p. 86) reassigned *Prenaster excentricus* (Wright, 1855) to *Peribrissus* in the belief that the two genera overlap based on the similarity of their upper test profile with highly eccentric anterior apex and four ethmolitic genital pores. Pomel’s statement (1887, p. 63) — that the number of genital pores in *Peribrissus* is unknown — seems to have been ignored by Stefanini, whose reference to four genital pores may have been based on details of Wright’s species. Giorgio (1923, p. 125), in describing *Peribrissus sotgiai* from Sardinia, accepted Stefanini’s finding that Wright’s *Prenaster* from Malta was a *Peribrissus*; noting that *P. sotgiai* has four gonopores, but that the right anterior one is poor and almost atrophied. These statements appear to have resulted in Mortensen (1951) and Fischer (1966) listing both genera as having four genital pores. However, of the eight genera now included in the family *Prenasteridae* by Smith et al. (2005), only *Peribrissus* and *Tripylus* Philippi, 1845 are listed as having three genital pores. Although both of these genera have a well-defined anterior sulcus, *Peribrissus* is easily distinguished from *Tripylus* by the markedly anterior location

of its apical disk compared to the central position in the latter. The lack of a sulcus and the presence of four genital pores in species of *Prenaster* clearly refute Stefanini’s reassignment of *Prenaster excentricus* to *Peribrissus*.

Peribrissus janiceae sp. nov.

Figures 2A–E, 3A–I, Table 1

Type material. Holotype and only known specimen, NMV P316528, from the early middle Miocene Glenforslan Formation (Batesfordian, Langian), Morgan Group, 7 km north-northeast of Murray River Lock 1, Blanchetown, South Australia [NMV locality PL3203].

Description. Test moderately large, ovate in outline with well-formed anterior sulcus; only known specimen 58.0 mm long, with maximum width of 52.0 mm (89.7%TL) occurring posterior of centre at 54.3%TL from anterior ambitus. Maximum test height 38.5 mm (66.4%TL) anterior of centre, but posterior of apical disk at 44.8%TL from anterior ambitus.

Adapical surface inflated with high, vertically convex anterior, gently curved ridge along interradial suture of interambulacrum 5 and prominent vertically truncated posterior. Laterally, sides gently curved at approximately 40° to the horizontal between dorsal ridge and well-rounded ambitus situated about one-third test height above the underside. Adoral surface posterior of peristome flat along centre line of labrum and plastron (fig. 2C–E).

Small, very closely spaced tubercles cover nearly all the test; smallest around ambitus and largest towards peristome.

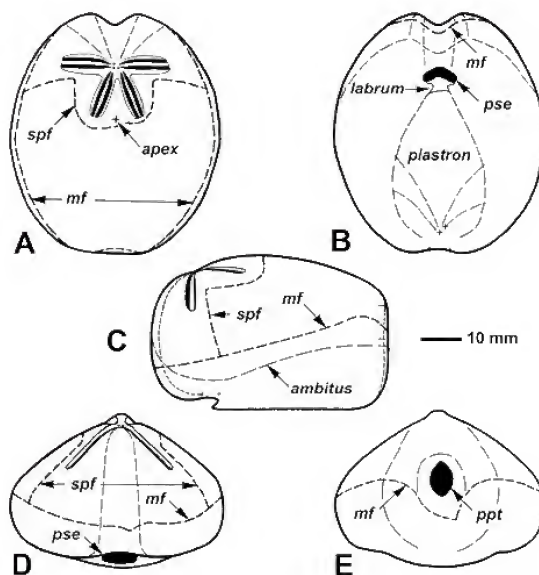


Figure 2. *Peribrissus janiceae* sp. nov. A–E, outline drawings of adapical, adoral, left lateral, anterior and posterior views of holotype NMV P316528, showing paths followed by marginal (mf) and semipetalous (spf) fascioles, and position of peristome (pse) and periproct (ppt).

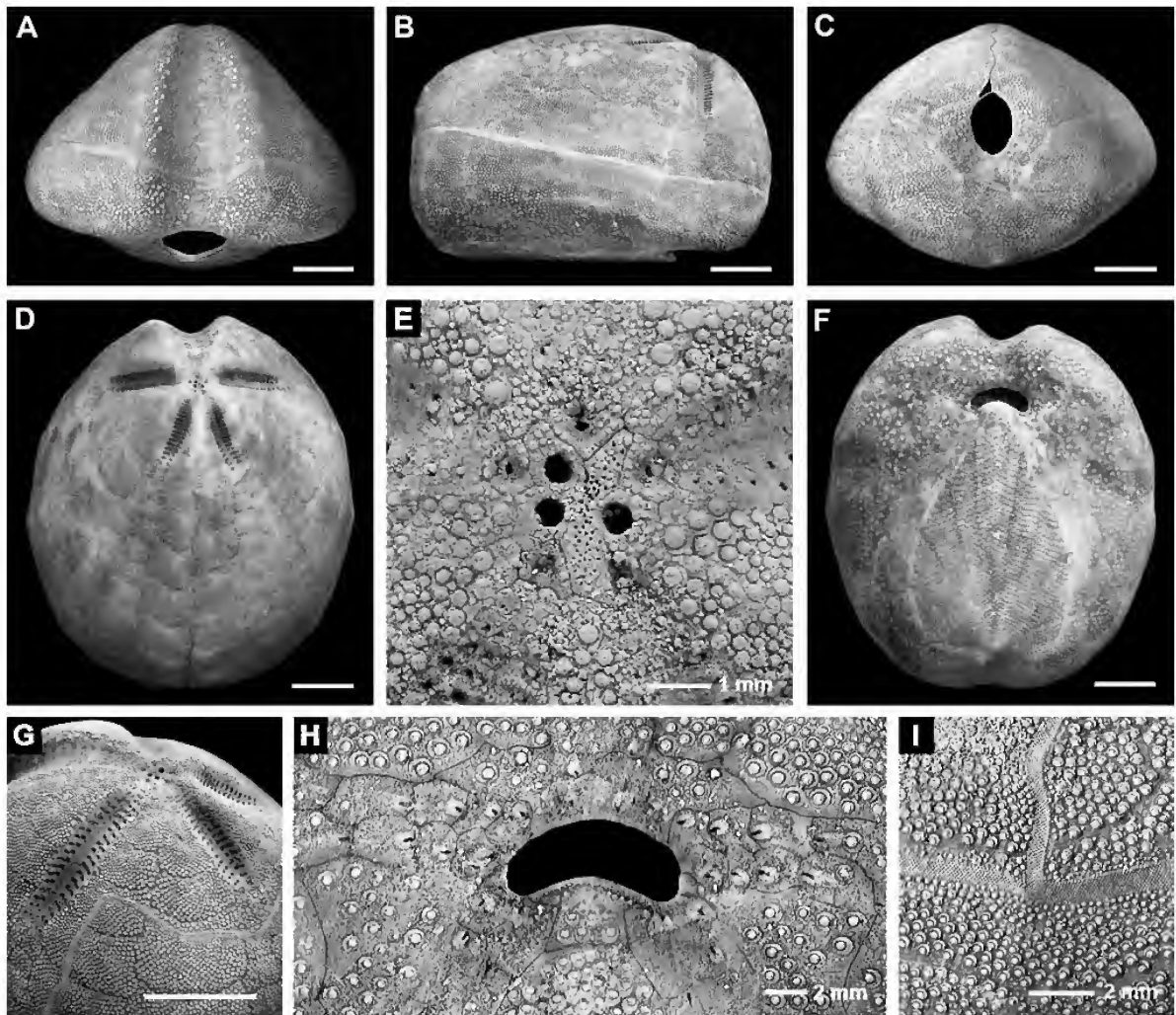


Figure 3. *Peribrissus janiceae* sp. nov. holotype NMV P316528. A–D and F, anterior, right lateral, posterior, adapical and adoral views; E, detail of apical disk; G, oblique left lateral view of semipetalous fasciole crossing interambulacrum 4, plates 7a, 8a, 9a and 9b; H, detail of peristome, labrum and phylodal plates; I, detail of junction between marginal and semipetalous fascioles on interambulacrum 1, plate 4b. Scale bars = 10 mm unless otherwise shown.

Tubercles in ambulacra II and IV first appear on plates 3a and b, and in I and V on plates 4a and b. By plates 5a and b, the size and spacing generally matches that of adjacent interambulacra. Largest tubercles with an approximate areole diameter of 1.0 mm occur on interambulacra 1 and 4 adjacent to adoral edge of plates 2a and b, aborally on plate 1, and along the adradial suture line between ambulacrum III and interambulacra 2 and 3 from the marginal fasciole to the apical disk. These tubercles have a perforate mamelon and crenulate platform but appear to lack a scrobular ring. Because of the very close spacing of these tubercles, miliary granules occur mainly towards the peristome and between the periproct and marginal fasciole in

interambulacrum 5 where the spacing between the larger tubercles increases. They also occur around the apical disk.

A well-defined marginal fasciole occurs just above the sloping ambitus, dipping sharply below the periproct posteriorly but crossing ambulacrum III anteriorly slightly below the ambitus at about 25%TH (see fig. 2). The semipetalous fasciole is only marginally indented between the posterior paired petals and crosses interambulacra 1 and 4 on plates 8/9 before descending transversely to join the marginal fasciole at right angles, posterior to the angle of the anterior paired petals (see fig. 3I). Although continuous, fasciole widths vary but maintain a fine tubercule (granule) density of about 100–120 per mm².

Table 1. Comparison of diagnostic features of *Peribrissus janiceae* sp. nov. with those of the type species of the genus, *P. sahelensis* Pomel, 1883, and *P. sotgiai* Giorgio, 1923.

Diagnostic feature	<i>Peribrissus janiceae</i> sp. nov.	<i>Peribrissus sahelensis</i> Pomel	<i>Peribrissus sotgiai</i> Giorgio
Width/length ratio of test	89.7%TL	Similar	Similar
Maximum width location	Marginally posterior at 54.3%TL	Marginally anterior, approx. 45%TL	Similar to <i>P. sahelensis</i>
Height/length ratio of test	66.4%TL	Not known	Approx. 54%TL
Maximum height location	Slightly anterior at 44.8%	Well anterior but posterior of apical disk, approx. 30%TL	Well posterior, approx. 68%TL
Anterior lateral profile	High, vertically convex	Slopes forward from apex at approx. 35°	Similar to <i>P. janiceae</i>
Posterior lateral profile	High vertical truncation	Oblique truncation	Oblique truncation
Adoral surface lateral profile	Flat, posterior of peristome	Unknown (type specimen compressed)	Slightly swollen posterior of centre
Sulcus	Max. depth/width ratio approx. 1:4.6, occurs below ambitus	Figured much deeper with a depth/width ratio of approx. 1:2.2	Figured far shallower and wider than <i>P. janiceae</i>
Apical system location and type	21%TL, ethmolitic, 3 gonopores (none in plate G2)	Approx. 33%TL, detail of apical system unknown (Pomel 1887). Stefenini (1911) incorrectly assumes 4 gonopores. This repeated by Mortensen (1950) and Fisher (1966).	Approx. average of 2 specimens 25%TL, ethmolitic. Giorgio's description refers to 4 gonopores but states the pore in G2 almost atrophied
Ambulacrum III, marginal tubercles	Not unduly prominent, situated just outside adradial sutures	Similar to <i>P. janiceae</i>	Larger, far more prominent with rows further apart
Detail of petals	Straight, parallel sided and sunken	Similar, but probably shallower	Similar
Length differentiation paired petals	Anterior petals 138% longer than posterior ones	Similar to <i>P. janiceae</i>	More equal, but posterior petals still shorter than anterior ones
Anterior paired petals divergence angle	175°	Approx. 135°	Described as 140°. Giorgio's figures, however, suggest divergence wider
Posterior paired petals divergence angle	315°	Approx. 295°	Similar to <i>P. janiceae</i>
Peristome	Reniform and slightly sunken	Insufficient information for comparison	Insufficient information for comparison
Periproct	Vertically elliptical at top of posterior truncation	Semicircular, assumed high on posterior truncation	Elliptical (axis not clear), high on posterior truncation
Fascioles, marginal and semipetalous	Marginal fasciole occurs just above sloping ambitus and is joined by semipetalous fasciole at right angles behind and below anterior paired petals	Similar, but with semipetalous fasciole shown angled forward at junction with marginal fasciole, apparently due to less oblique divergence of anterior petals	Insufficient information for comparison, as stated to be only visible in some places

Apical system situated well anterior of centre at 21.0% TL from anterior ambitus to centre of disk and is level with proximal end of paired petals. Ethymolitic with three gonopores, no gonopore in plate G2, and approximately 60 hydropores fairly evenly spaced over the latter's length.

Paired petals straight, parallel sided, sunken, open distally and devoid of tubercles. Anterior paired petals 138% longer than posterior pair, extending 50% of the radius (28.0%TL)

measured along the surface of the perradial suture from centre of ocular to ambitus. Anterior paired petals diverge at 175° and contain 23/24 pore pairs, posterior petals 315° and 20/21 pairs. Outer pores elliptical, inner pores slightly smaller and more tear shaped. Zone between inner and outer pores approximately equal in width to outer pores, pairs not conjugate. Interporiferous zone marginally narrower than poriferous zones.

Ambulacrurum III depressed for its full length below

adjacent interambulacra, reaching a maximum depth of 3 mm (5.2%TL) below the anterior ambitus. Pore pairs are visible adapically between the ocular plate and approximately one-third of the radius to the anterior ambitus. Adapically, the pore pairs are angled inwards at approximately 45° to the perradial suture but gradually become monoserial halfway towards the anterior ambitus. The ambulacrum is covered with closely spaced small tubercles and miliary granules, the former gradually increasing in diameter adorally.

Peristome reniform and slightly sunken, longitudinal dimension 4 mm (6.9%TL), width 8.6 mm (14.8%TL), anterior edge situated 12.4 mm (21.4% TL) from ambitus. Phyllodes unipored with periporal areas protuberant. Basicoronal plates amphiplaceous.

Labrum small, wider than long, covered with small tubercles and flared anteriorly where bordered by a smooth raised rim (fig. 3H). Curved anterior edge projects over the peristome for about one-third of the latter's length. Posterior edge does not extend beyond the first adjacent ambulacral plates. Plastron wide, long, and covered with rows of closely spaced angular tubercles without interstices. Maximum width of plastron (45%TW) occurs about three-quarters of the test length from the anterior ambitus.

Periproct elliptical shaped with slightly pointed upper and lower junction with interradian suture, height 8.0 mm (13.8%TL), width 5.0 mm (5.6%TL). Underside of vertical opening situated high above base of test (44.2%TH) on truncated posterior surface. Subanal surface slightly depressed.

Etymology. Named for Janice Krause of Hamilton, Victoria, an exceptionally dedicated fossil echinoid collector.

Remarks. Comparison of *Peribrissus janiceae* sp. nov. with the type species *P. sahelensis* from Algeria and *P. sotgiai* from Sardinia is complicated by the lack of detailed descriptions, comparative measurements and illustrations of many of the important diagnostic features of the latter two species. The difficulty is compounded by the excellent preservation of detail found on the single specimen of *P. janiceae* and the large difference in size between specimens of the three species, with *P. sahelensis* approximately twice the length and width of *P. janiceae* and four times that of *P. sotgiai*. Where possible, diagnostic features of the three species are compared in table 1, based on the descriptions of Pomel (1887), Giorgio (1923) and Stefanini (1911), together with approximate measurements taken from their illustrations of the partial and poorly preserved type specimens.

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References

- Agassiz, A. 1904. The panamic deep sea echini. *Memoirs of the Museum of Comparative Zoology at Harvard College* 31: 1–243.
- Agassiz, L. 1840. *Catalogus systematicus Ectyporum Echinodermatum fossilium Musei Neocomiensis, secundum ordinem zoologicum dispositus; adjectis synonymis recentioribus, nec non stratis et locis in quibus reperiuntur. Sequuntur characteres diagnostici generum novorum vel minus cognitorum.* Petitpierre, Neuchâtel, 20 pp.
- Agassiz, L. and Desor, E., 1847. Catalogue raisonné des familles, des genres et des espèces de la classe des échinodermes. *Annales des Sciences naturelles*, series 3, Zoologie 8: 5–35.
- Desor, E. 1853. Notice sur les échinides du terrain nummulitique des Alpes avec les diagnoses et plusieurs espèces et genres nouveaux. *Actes de la Société Helvétique des Sciences Naturelles* 38: 270–279.
- Duncan, P. M. 1877. On the Echinodermata of the Australian Cainozoic (Tertiary) deposits. *Quarterly Journal of the Geological Society of London* 33(1): 42–73, pls 3–4.
- Durham, J. W. and Melville, R. V. 1957. A classification of echinoids. *Journal of Paleontology* 31: 242–272.
- Fischer, A. G. 1966. Spatangoids. Pp. U543–U628 in Moore R. C. (ed.), *Treatise on Invertebrate Paleontology, Part U Echinodermata* 3(2). The Geological Society of America Inc. and The University of Kansas Press.
- Giorgio, A. Di 1923. Echinidi Miocenici della Sardegna. *Atti della Società Toscana di Scienze Naturali residente in Pisa*, 35: 116–130, pl. 2(1).
- Gregory, J. W. 1890. Some additions to the Australian Tertiary Echinoidea. *The Geological Magazine* 27 (new series, decade 3, vol. 7, no. 11): 481–492, pls 1314.
- Holmes, F. C., Ah Yee, C. and Krause, J. 2005. Two new Middle Miocene spatangoids (Echinoidea) from the Murray Basin, South Australia. *Memoirs of Museum Victoria* 62(1): 91–99.
- ICZN (International Commission on Zoological Nomenclature) 1999. *International Code of Zoological Nomenclature*, 4th edn. International Trust for Zoological Nomenclature, London, 306 pp.
- Kroh, A. and Smith, A. B. 2010. The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology* 8 (2): 141–212.
- Lambert, J. 1905. Notes sur quelques Echinides éocéniques de l'Aude et de l'Hérault. In: L. Doncieux (ed.), *Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Hérault. Annales de l'Université de Lyon, Nouvelle Série, I. Sciences, Médecine* 17: 129–164.
- Lambert, J. and Thiéry, P. 1925. *Essai de nomenclature raisonnée des échinides*. Librairie L. Ferrière, Charmont, fasc. 8–9, 513–607, pls 12–13, 15.
- Lukasik, J. J. and James, N. P. 1998. Lithostratigraphic revision and correlation of the Oligo–Miocene Murray Supergroup, western Murray Basin, South Australia. *Australian Journal of Earth Sciences* 45: 889–902.
- McGowran, B. and Li, Q. 1994. Miocene oscillation in southern Australia. *Records of the South Australian Museum* 27: 197–212.
- McNamara, K. J. and Philip, G. M. 1984. A revision of the spatangoid echinoid *Pericosmus* from the Tertiary of Australia. *Records of the Western Australian Museum* 11(40): 319–356.

- Markov, A. V. and Solov'ev, A. N. 2001. Morskije ezhi semeystva Paleopneustidae (Echinoidea, Spatangoida) morfologiya, sistema, filogeniya. *Rossiyskaya Akademiya nauk, Trudy Paleontologicheskogo Instituta* 280: 1–109.
- Mortensen, T. 1951. *A monograph of the Echinoidea* 5(2). Spatangoida 2. Amphisternata 2. Spatangidae, Loveniidae, Pericosmidae, Schizasteridae, Brissidae. C. A. Reitzel, Copenhagen, 593 pp.
- Philippi, R. A. 1845. Beschreibung einiger neuen Echinodermen nebst kritischen Bemerkungen über einige weniger bekannte Arten. *Archiv für Naturgeschichte* 11(1): 344–359.
- Pomel, A. 1869. *Revue des Échinodermes et de leur classification pour servir d'introduction à l'étude des fossils*. Deyrolle, Paris: 67 pp.
- Pomel, A. 1883. *Classification méthodique et Genera des Échinides vivants et fossiles*. Adolphe Jordan, Alger, 131 pp., 1 pl.
- Pomel, A. 1887. *Paléontologie ou descriptions des animaux fossils de l'Algérie. Zoophytes 2e Fascicule — Echinodermes 2e Livraison*. Imprimerie de l'Association Ouvrière, P. Fontana et Cie. Alger, 344 pp. + 120 pls.
- Smith, A. B. 1984. *Echinoid Palaeobiology*. George Allen & Unwin, London, 190 pp. + fig. A.1.
- Smith, A. B. and Stockley, B. 2005. Fasciole pathways in spatangoid echinoids: a new source of phylogenetically informative characters. *Zoological Journal of the Linnean Society* 144: 15–35.
- Smith, A. B., Stockley, B. and Godfrey, D. 2005. *Spatangoida*. In: Smith, A. B. (ed.). *The Echinoid Directory*. www.nhm.ac.uk/palaeontology/echinoids (accessed 10 April 2011).
- Stefanini, G. 1911. Note Echinologiche II. *Peribrissus excentricus* (Wright sp.). *Rivista Italiana di Paleontologia e Stratigrafia* 17(4): 85–88.
- Termier, H. and Termier, G. 1953. Classe des Echininides. Pp. 857–947 in Masson et cie (eds), *Traité de Paléontologie, Tome 3*. Saint-Germain, Paris.
- Wright, T. 1855. On fossil Echinodermata from the island of Malta; with notes on the stratigraphical distribution of the fossil organisms in the Maltese beds. *Annals and Magazine of Natural History, Series 2*, 15: 101–127.

The paracaudinid sea cucumbers of Australia and New Zealand (Echinodermata: Holothuroidea: Molpadida: Caudinidae)

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Abstract

O'Loughlin, P. M., Barmos, S. and VandenSpiegel, D. 2011. The paracaudinid sea cucumbers of Australia and New Zealand (Echinodermata: Holothuroidea: Molpadida: Caudinidae). *Memoirs of Museum Victoria* 68: 37–65

The four *Paracaudina* Heding species reported in Australia are reviewed: *Paracaudina australis* (Semper); *Paracaudina chilensis* (Müller); *Paracaudina luticola* Hickman; *Paracaudina tetrapora* (H. L. Clark). The New Zealand species *Paracaudina coriacea* (Hutton) is raised out of synonymy with the Chilean species *Paracaudina chilensis* (Müller). Both *Paracaudina chilensis* (Müller) and *Paracaudina coriacea* (Hutton) occur in New Zealand. The synonymy of the Chinese and Japanese species *Paracaudina ransonnetii* (Marenzeller) with *Paracaudina chilensis* (Müller) is maintained. Five new Caudinidae species are erected for Australia, with authors O'Loughlin and Barmos: *Paracaudina ambigua*, *Paracaudina bacillis*, *Paracaudina cuprea*, *Paracaudina keablei*, *Paracaudina tripoda*. A key is provided for *Paracaudina* species in Australia and New Zealand.

Keywords

Sea cucumber, Molpadida, Caudinidae, *Paracaudina*, new species, synonymies, Australia, New Zealand, key.

Introduction

Museum Victoria holds numerous specimens of Caudinidae sea cucumbers, most specimens collected from Victorian beaches after storms. Rowe 1982 recorded a “*Paracaudina* sp.” from Port Phillip Bay in Victoria and southern Western Australia. This species is represented by numerous specimens from southern Australian waters, and we erect a new species. We have examined collections of *Paracaudina* Heding, 1932 from the Australian, South Australian, Western Australian and New Zealand Museums, and we review all of the species of this genus in Australian and New Zealand waters. As an outcome of this review we erect five new species of *Paracaudina*. Our systematic study is based on traditional morphological characters as there are to date no adequate molecular genetic data.

Four potential Australian and New Zealand species of *Paracaudina* have been intensively studied: *Paracaudina australis* (Semper, 1868) with type locality Australia; *Paracaudina chilensis* (Müller, 1850) with type locality Chile; *Paracaudina coriacea* (Hutton, 1872) with type locality New Zealand; *Paracaudina ransonnetii* (Marenzeller, 1881) with type locality China. Their morphology and systematic status have been researched and debated by numerous authors: Théel 1886; H. L. Clark 1908, 1935; Mortensen 1925; Hozawa 1928; Ohshima 1929; Heding 1931, 1933; Pawson 1963; Pawson and

Liao 1992. Most recently Pawson 1963 has summarised what has been debated, and agreed with the authors who considered *P. coriacea* (Hutton) to be a junior synonym of *P. chilensis* (Müller). We reject this synonymy, judging that *Paracaudina coriacea* (Hutton) is a good species. But at the same time we have found that *Paracaudina chilensis* (Müller) also occurs in New Zealand waters, and one or possibly more undescribed *Paracaudina* species. A comprehensive review of the many *Paracaudina* specimens held in New Zealand will follow this work. In reporting on the molpadid sea cucumbers of China, Pawson and Liao 1992 agreed with the synonymy of the China and Japan species *P. ransonnetii* (Marenzeller) with *P. chilensis* (Müller). We agree with this synonymy. However, we note that some of these species distributions are such that molecular genetic data may reveal that some of these species are paraphyletic.

Our experience of looking at a range of material leads us to agree with H. L. Clark 1935 that there is considerable variation in morphological form amongst *Paracaudina* specimens that are conspecific, including ossicle form. And we agree also that, although there is considerable variation in ossicle form in the same and conspecific specimens, predominant ossicle form does provide a reliable guide to species identity.

Methods

For scanning electron microscope (SEM) observations by Didier VandenSpiegel ossicles were cleared of associated soft tissue in commercial bleach, air-dried, mounted on aluminium stubs, and coated with gold. Observations were made using a JEOL JSM-6480LV SEM. Measurements were made with Smile view software. Photos of preserved specimens by Shari Barmos were taken with a Nikon D70 DSLR camera, using a Nikon micro 60 mm lens.

Abbreviations

AM Australian Museum (with registration prefix J).
MRG Marine Research Group of the Field Naturalists Club of Victoria.
NMV Museum Victoria (with registration prefix F).
NIWA New Zealand Institute of Water and Atmospheric Research.
SAM South Australian Museum (with registration prefix K).
WAM Western Australian Museum (with registration prefix Z).

Numbers in brackets after registrations refer to the number of specimens in a registered lot.

Spelling correction

Some authors have misspelled the species name *ransonnetii*, and the correct spelling only is used throughout our work.

Key to the Australian and New Zealand species of *Paracaudina* Heding

1. Ossicles in body wall small irregular rods only
Paracaudina bacillis O'Loughlin and Barmos sp. nov.
(southern Australia)
- Ossicles in body wall include small buttons or perforated plates or thick cups **2**
2. Ossicles in mid-body predominantly small rods and loops, and in caudal end predominantly spinous perforated plates *Paracaudina ambigua* O'Loughlin and Barmos sp. nov. (central Western Australia)
- Ossicles similar in mid-body and caudally **3**
3. Ossicles in body wall predominantly octagonal plates with central perforation over which there is a bridging box on the basal side and cross on the outer side **4**
- Ossicles in body wall rarely octagonal plates with box and cross bridges, or such ossicles completely absent **6**
4. Octagonal plates predominantly with marginal bluntly pointed projections and knobs; perforations not significantly smaller in collective area than the surface area of the plate; body with long thin tail *Paracaudina chilensis* (Müller, 1850) (circum-Pacific, north-western Australia)
- Octagonal plates predominantly with rounded margin, margin lacking bluntly pointed projections and knobs ... **5**

5. Ossicles predominantly thick and button-like, perforations significantly smaller in collective area than the plate surface area; body with long thin tail *Paracaudina coriacea* (Hutton, 1872) (New Zealand)
- Ossicles predominantly thin-walled and open mesh-like, perforations not significantly smaller in collective area than the plate surface area; body with short thin tail
Paracaudina keablei O'Loughlin and Barmos sp. nov.
(north-eastern Australia)
6. Ossicles in body wall predominantly thick-walled with 4 perforations **7**
- Ossicles in body wall include irregular plates and buttons with irregular perforations, with marginal and surface knobs and pointed projections variably present; plates with up to 12 perforations **8**
7. Ossicles in body wall predominantly thick, shallow concave crossed cups *Paracaudina luticola* Hickman, 1962 (southern Australia)
- Ossicles in body wall predominantly thick, knobbed and irregularly oval flat plates *Paracaudina tetrapora* (H. L. Clark, 1914) (southern Australia)
8. Ossicles in body wall predominantly buttons with smooth rounded lateral margin, short thick blunt surface spines, frequently with central perforation bridged by a tripod of rods ... *Paracaudina tripoda* O'Loughlin and Barmos, sp. nov. (north-eastern Australia)
- Ossicles in body wall plates, most with lateral and surface rounded marginal spines and knobs **9**
9. Deeper mid-body wall with irregular rods, less than 50 μm long; colour never yellowish-red (rusty)
Paracaudina australis (Semper, 1868) (north-eastern Australia)
- Deeper mid-body wall lacking irregular rods; larger specimens increasingly yellowish-red (rusty) in colour
Paracaudina cuprea O'Loughlin and Barmos sp. nov.
(southern Australia)

Remarks. The remaining subspecies and species of *Paracaudina* Heding, 1932 that are not included in this key are: *Paracaudina chilensis obesacauda* (H. L. Clark, 1908), a central American east Pacific and west Atlantic subspecies, retained with subspecific status solely on geographical grounds by Pawson et al. 2001; *Paracaudina delicata* Pawson and Liao, 1992, from the Gulf of Tonkin, has thin-walled *chilensis*-like ossicles, with box and cross bridging a central perforation, and fine digitiform projections around the ossicle margin.

Order Molpadida Haeckel, 1896

Diagnosis (emended from Pawson and Liao 1992). Tentacles 15, digitate; body stout, lacking tube feet, usually with an evident tail; anal papillae, tentacle ampullae and respiratory trees present; ossicles may include tables, cups, rods, perforated plates and modified anchors; phosphatic bodies often present.

Remarks. Rods may be present with perforated plates, as in *Paracaudina australis* (Semper, 1868), and rods are not necessarily fusiform (spindle-shaped). We have emended the diagnosis of Pawson and Liao 1992 in these two respects.

Family Caudinidae Heding, 1931

Diagnosis (emended from Pawson and Liao 1992). Tentacles without a terminal digit, and with one or two pairs of lateral digits; tail sometimes inconspicuous; ossicles may include large tables, crossed cups, perforated plates and irregular rods; phosphatic bodies usually absent.

Remarks. We have emended the statement concerning which ossicles may be present, but we have not changed the ossicle types listed.

Paracaudina Heding, 1932

Figures 1f, 5c–e, 7, 8, 12a, b

Pseudocaudina Heding, 1931: 283.

Paracaudina Heding, 1932: 455–456.

Type species. *Molpadia chilensis* Müller, 1850 (subsequent designation by H. L. Clark 1935).

Other included species. *Paracaudina ambigua* O'Loughlin and Barmos sp. nov.; *P. australis* (Semper, 1868); *P. bacillis* O'Loughlin and Barmos sp. nov.; *P. coriacea* (Hutton, 1872); *P. cuprea* O'Loughlin and Barmos sp. nov.; *P. delicata* Pawson and Liao, 1992; *P. keablei* O'Loughlin and Barmos sp. nov.; *P. luticola* Hickman, 1962; *P. chilensis obesacauda* (H. L. Clark, 1908); *P. tetrapora* (H. L. Clark, 1914); *P. tripoda* O'Loughlin and Barmos sp. nov.

Diagnosis. Cylindrical form, smooth or wrinkled body wall; tentacles 15, each with 2 pairs of digits (figs 1f, 5c); posterior end of body with caudal taper or discrete thin tail; tail may be short or long; 5 radial triangular non-calcareous anal valves, each with up to 4–5 pairs of marginal digitiform papillae, terminal ones longest (fig. 5d); radial plates of calcareous ring with two anterior lateral low blunt projections, one with small notch, posterior digitiform prolongation about half the length of the plate, prolongation divided by terminal notch of variable depth or deeper division (fig. 12a); interrarial plates with anterior central blunt point, posterior end truncated (fig. 12a); dorsal short to long tubular stone canal with terminal madreporite, free in coelom or attached to pyloric mesentery (specimen NMV F174894); single ventral, elongate, tubular to globular polian vesicle, usually with dark reddish-brown colouration; longitudinal muscles broad, flat, with distinct longitudinal division (fig. 5e); retractor muscles formed by pair of in-turned outer margins of divided longitudinal muscles (fig. 5e); gonad tubules usually branched, in tufts on each side of dorsal mesentery (fig. 5e); right branch of respiratory tree extending in the coelom to the calcareous ring; ossicles may be concave or flat, thick crossed and knobbed cups, thick knobbed perforated plates, octagonal plates with large central perforation and cross or tripod bridging one side and sometimes square the other side (figs 7, 8, 12b), perforated smooth and knobbed and spinous plates with variably developed secondary layering, and

irregular rods; ossicles never tables; phosphatising of ossicles and calcareous ring may occur, and a red to brown to yellow pigment may occur in the body wall.

Remarks. A comprehensive diagnosis of genus *Paracaudina* Heding, 1932 is provided to avoid diagnoses of species with repetition of characters that all have in common. We recognise that some of the characters listed in this diagnosis of *Paracaudina* are shared with other genera and at family and possibly order level.

Paracaudina ambigua O'Loughlin and Barmos sp. nov.

Figure 1a, 2

Material examined. Holotype. Western Australia, Shark Bay, FWA–WAM RV *Naturaliste* Shark Bay Survey II Feb / Mar 2003, stn 13/173/P, 24°47.02'S 113°21.97'E to 24°46.48'S 113°22.08'E, 24 m, 6 Mar 2003, S. Morrison and S. M. Slack-Smith, WAM Z29767.

Paratype. Western Australia, Ningaloo Marine Park, AIMS RV *Solander*, stn RVS 4545–D069, 23°48'S 113°30'E, 33 m, 1 Feb 2008, M. Salotti and S. M. Slack-Smith, WAM Z23331 (1).

Diagnosis. *Paracaudina* species up to 45 mm long (holotype, caudal taper but anal end and valves missing), body up to 15 mm high (body flattened laterally); body wall thick, soft to semi-gelatinous, white (preserved); posterior body with caudal taper to short discrete tail (evident in paratype); ossicles different mid-body and caudally; mid-body ossicles predominantly small irregular rods, frequently forming a single loop, or small plates with up to 4 perforations, these ossicles up to 40 µm long; rare mid-body irregularly oval perforated plates with spinous margin and some secondary bridging, about 64 µm long; caudal ossicles irregularly oval to round to octagonal perforated plates, long pointed spinous margin, surface spines and bridges and secondary development, some plates *chilensis*-like with box and cross bridges over central perforation, caudal ossicles typically 56–64 µm long.

Type locality. Central Western Australia, Shark Bay.

Distribution. Central Western Australia, Shark Bay, Ningaloo Marine Park; 24–33 m.

Etymology. From the Latin *ambiguus* (of double meaning, uncertain), feminine *ambigua*, referring to the generic uncertainty created by the presence of *Acaudina*-like ossicles mid-body and *Paracaudina*-like ossicles posteriorly.

Remarks. *Paracaudina ambigua* O'Loughlin and Barmos sp. nov. is distinguished diagnostically amongst *Paracaudina* species by having fine irregular rod and loop ossicles in the mid-body wall and marginally spinous *chilensis*-like plate ossicles in the caudal region, some with the characteristic cross and box bridges over a central perforation. Both specimens are in poor condition, but the ossicles are in excellent condition and characterise the new species. Distal pairs of digits are evident on a few tentacles of the holotype, but the condition of the tentacles is such that a second pair is not clearly evident on any tentacle. The caudal part is missing from the holotype, but a distinct narrow tail and soft anal valves are present on the paratype (18 mm long).

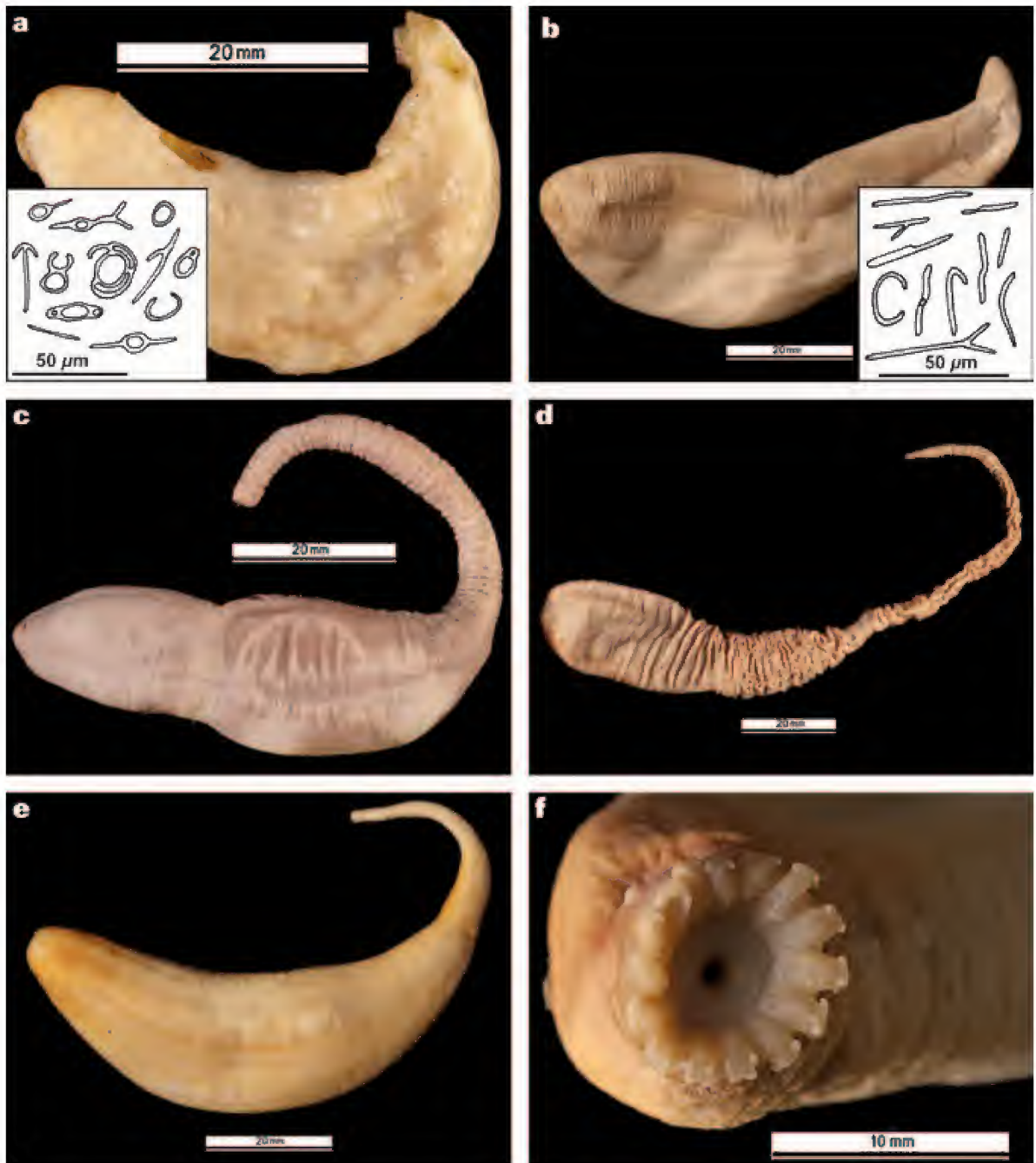


Figure 1. Photos of preserved specimens of species of *Paracaudina* Heding, 1932: a, holotype of *P. ambigua* O'Loughlin and Barmos sp. nov. (insert with drawings of rod and loop ossicles from the mid-body wall; WAM Z29767); b, *P. australis* (Semper, 1868) (insert with drawings of rod ossicles from the mid-body wall; AM J13583); c, *P. chilensis* (Müller, 1850) (WAM Z5638); d, *P. coriacea* (Hutton, 1872) (NIWA 70955); e, *P. coriacea* (Hutton, 1872) (AM J12290); f, mouth and tentacles of *P. coriacea* (Hutton, 1872) (NIWA 70954).

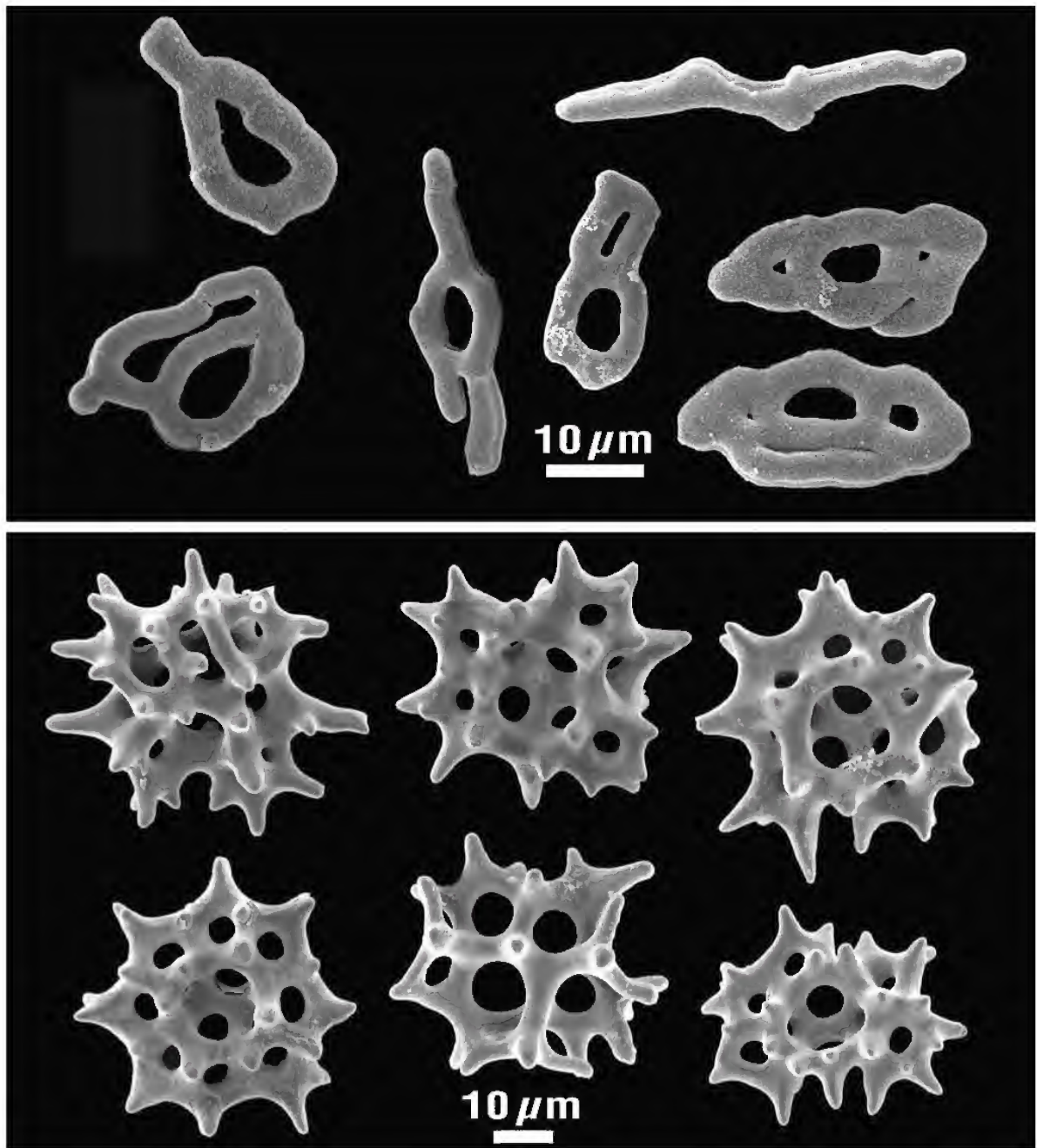


Figure 2. SEM images of ossicles from the holotype of *Paracaudina ambigua* O'Loughlin and Barmos sp. nov. from Shark Bay, central Western Australia (WAM Z29767): upper, forms of predominant ossicles from the mid-body wall; lower, forms of ossicles from the caudal body wall (rarely occurring *chilensis*-like ossicles with cross and box bridging shown lower top right and lower bottom left).

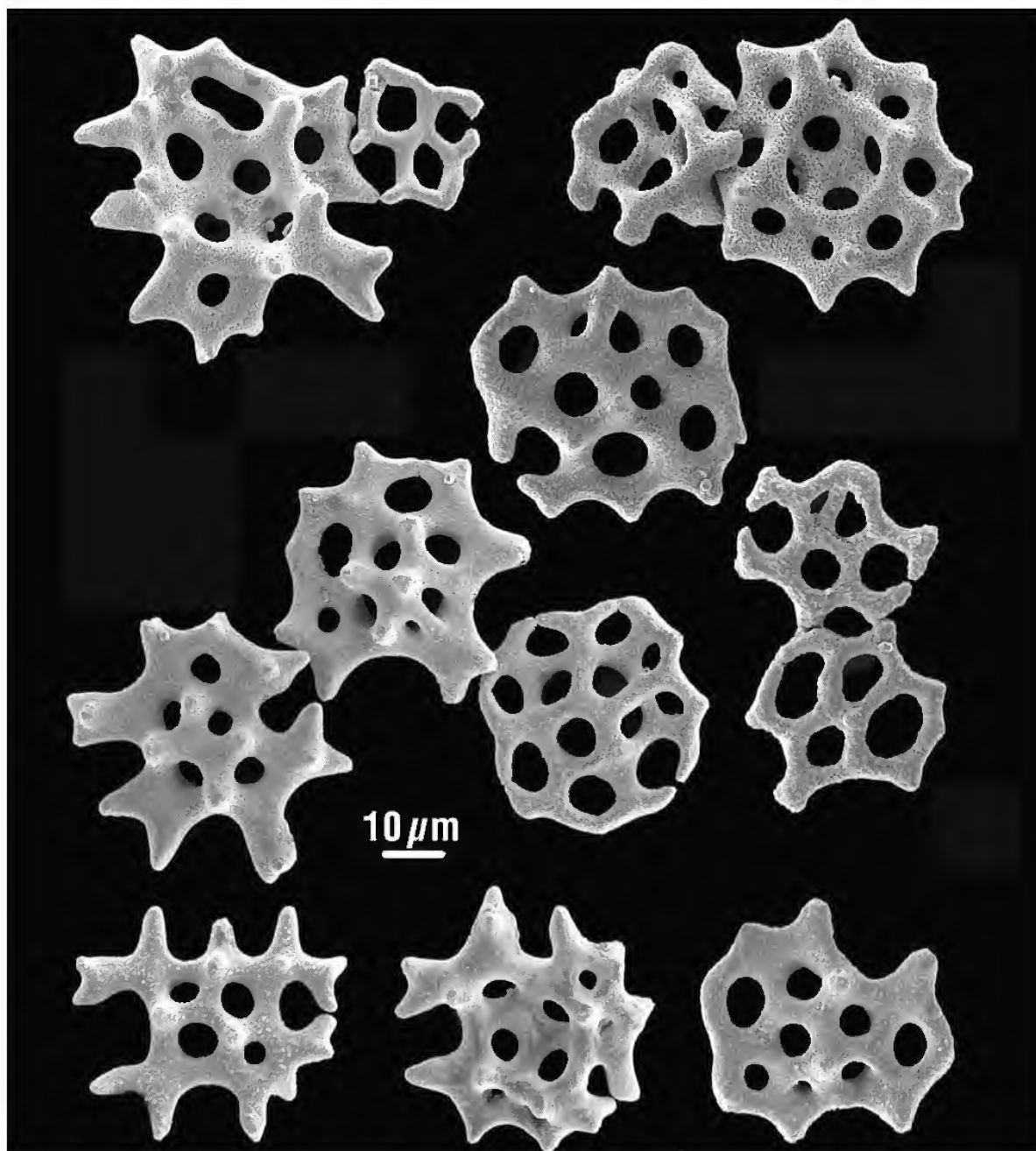


Figure 3. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina australis* (Semper, 1868) from Dunwich, Moreton Bay, south-east Queensland (AM J13583). Rarely occurring *chilensis*-like ossicle with cross and box bridging shown top right.

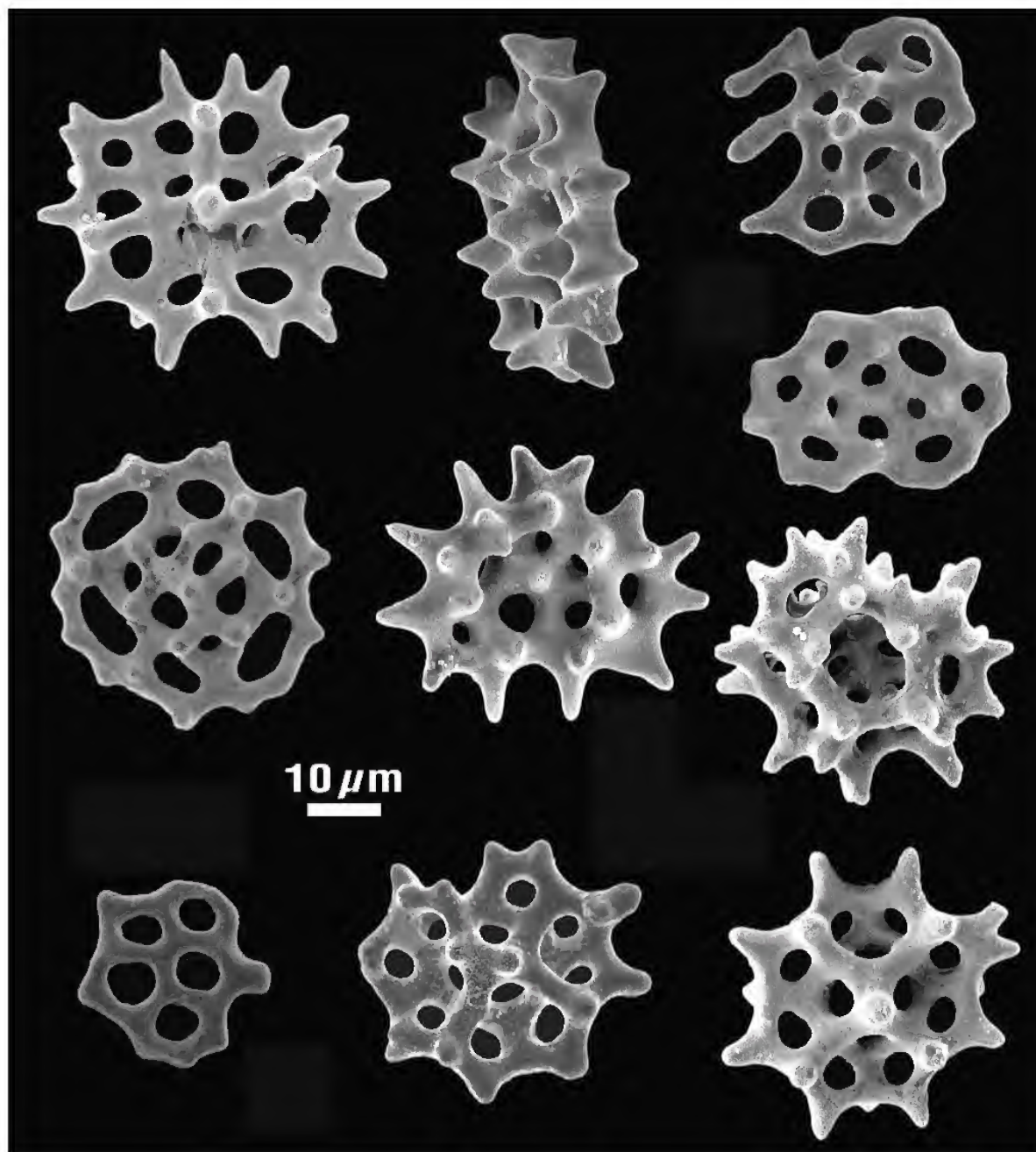


Figure 4. SEM images showing variation in form of ossicles from the mid-body wall of a specimen of *Paracaudina australis* (Semper, 1868) from Dunwich, Moreton Bay, south-east Queensland (AM J13583). Rarely occurring *chilensis*-like ossicle with cross and box bridging shown bottom right.

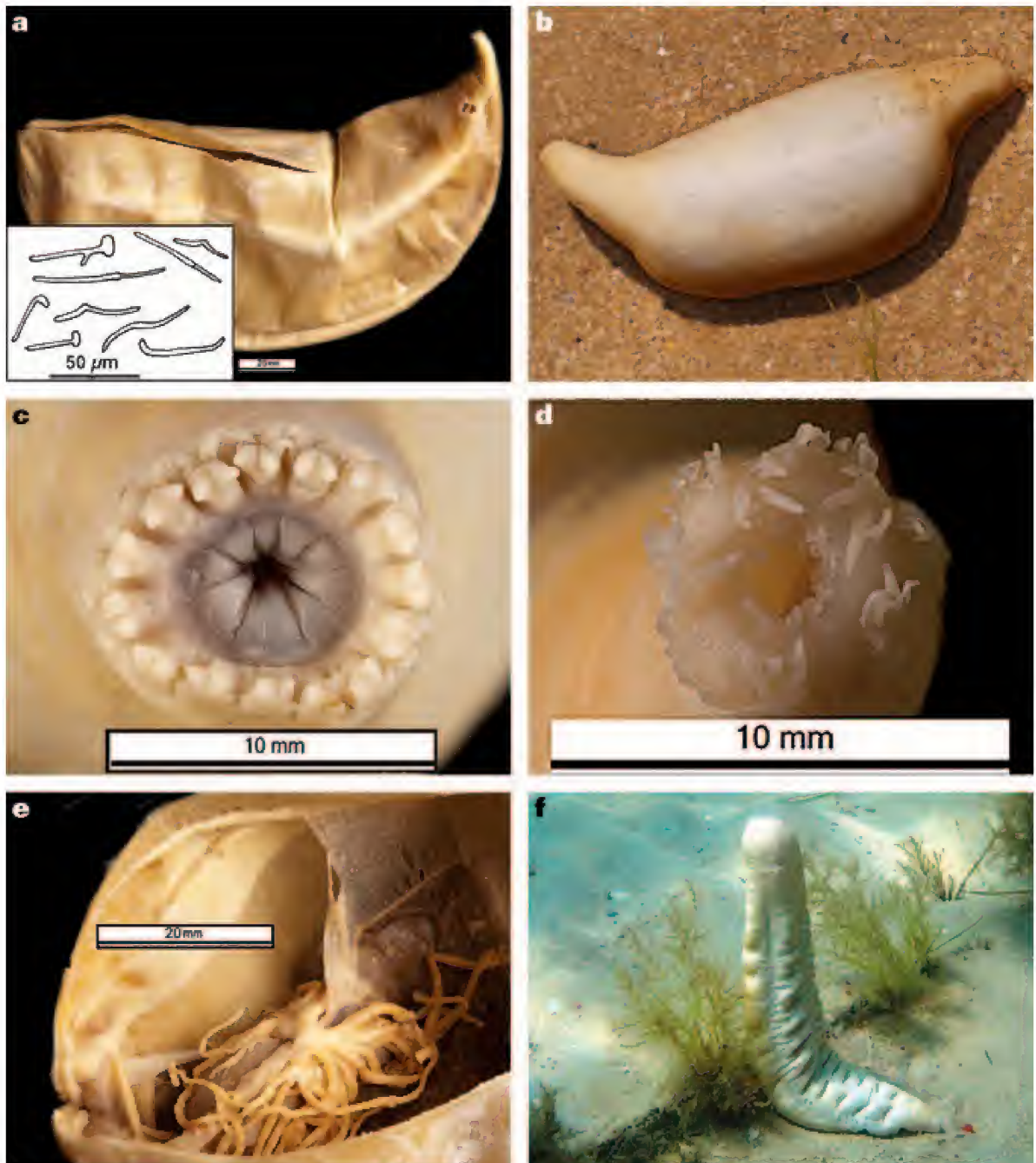


Figure 5. Photos of *Paracaudina bacillis* O'Loughlin and Barmos sp. nov.: a, preserved holotype specimen (insert with drawings of rods from the mid-body wall; NMV F151853); b, photo of live holotype (oral end right; photo by L. Altoff and A. Falconer); c, mouth and tentacles of paratype (NMV F174894); d, anal valves and papillae (holotype); e, dorsal mesentery with tufts of gonad tubules on both sides, divided flat longitudinal muscle with thin retractor muscle (holotype); f, live specimen spawning, Port Phillip Bay, Rye Pier, 4 m, 10 Nov 2007 (photo by D. McKenzie).



Figure 6. *Paracaudina bacillis* O'Loughlin and Barmos sp. nov. a, b, SEM images of rod ossicles from the mid-body wall of a paratype from Westernport Bay, Victoria (NMV F174893); c, photo of live specimen in Blairgowrie Marina, Port Phillip Bay, at 5 m depth (photo by J. Finn, 18 June 2011).

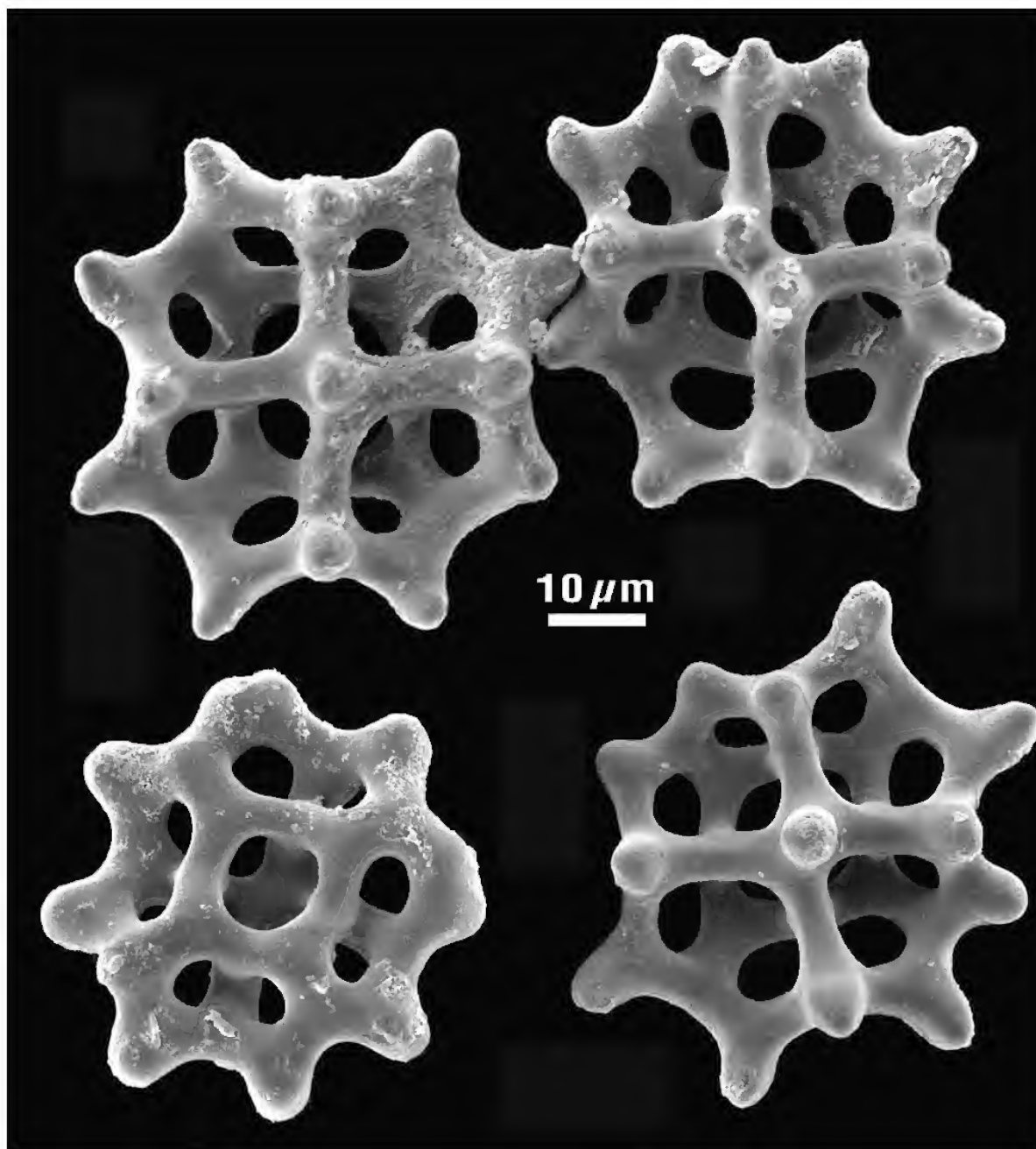


Figure 7. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina chilensis* (Müller, 1850) from Eighty Mile Beach, NW Australia (WAM Z5640).

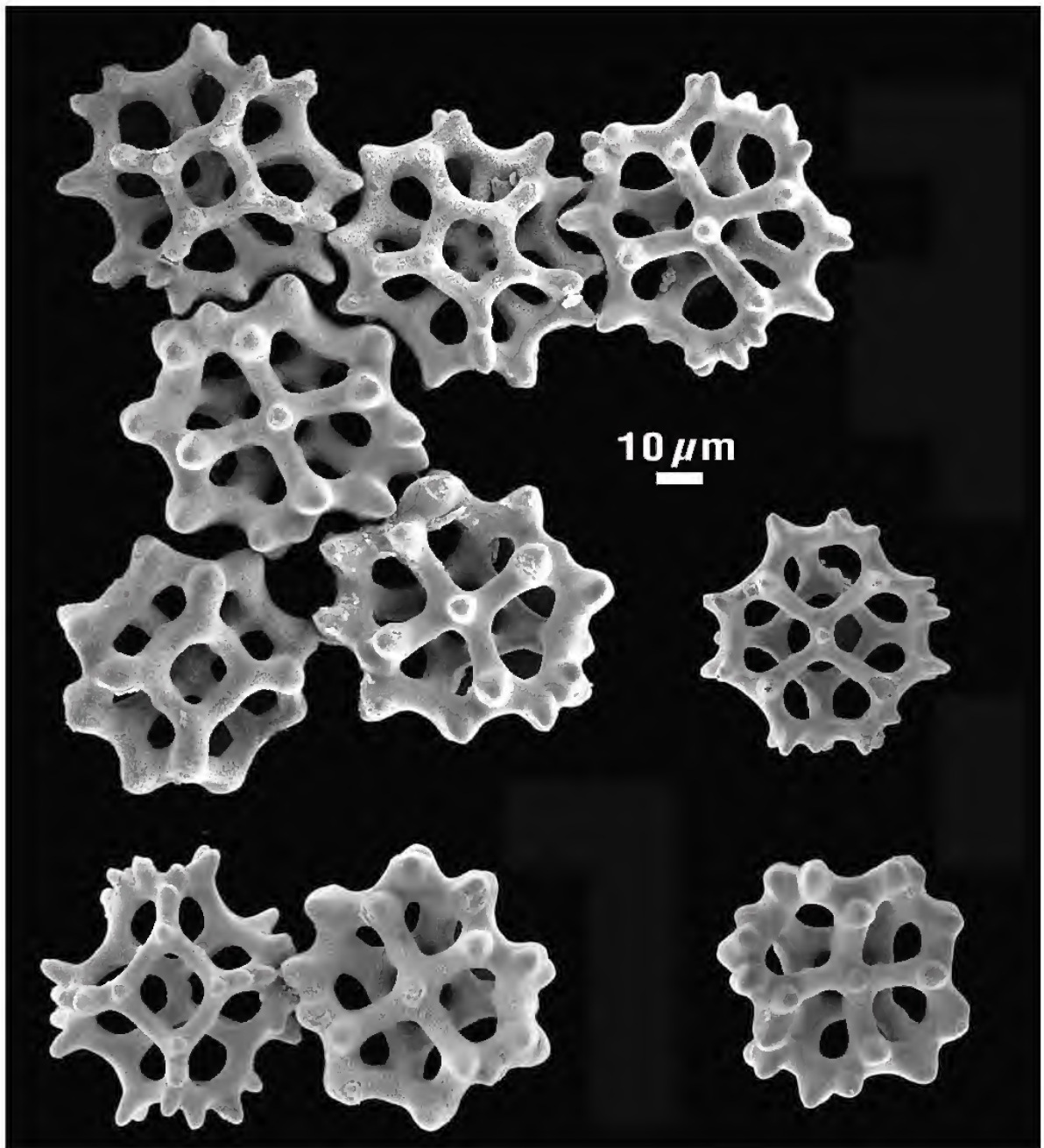


Figure 8. SEM images of ossicles from the mid-body wall of a small specimen of *Paracaudina chilensis* (Müller, 1850) from Tasman Bay, South Island, New Zealand (NIWA 70956).

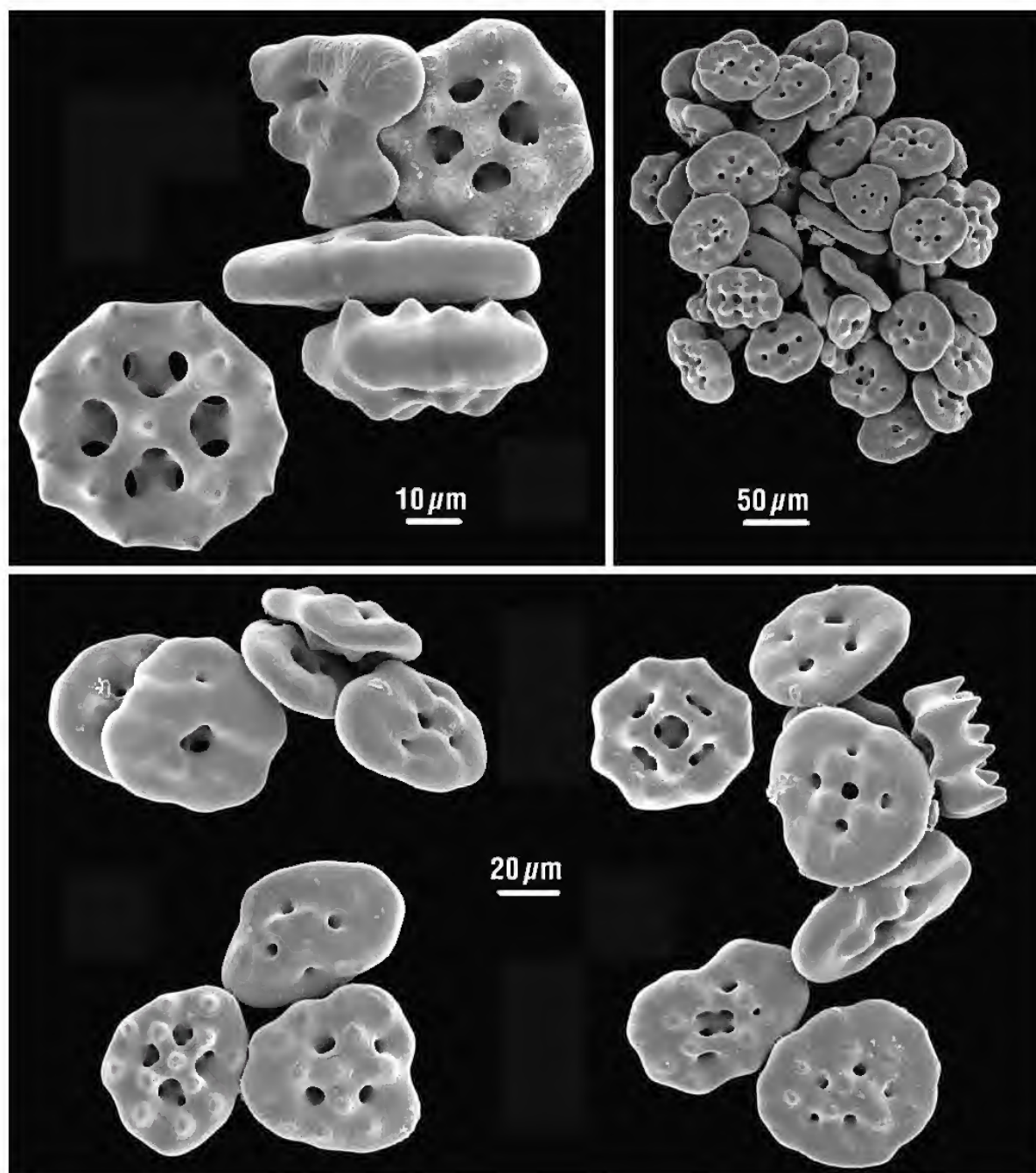


Figure 9. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina coriacea* (Hutton, 1872) from the west coast of the South Island, New Zealand (AM J12290).

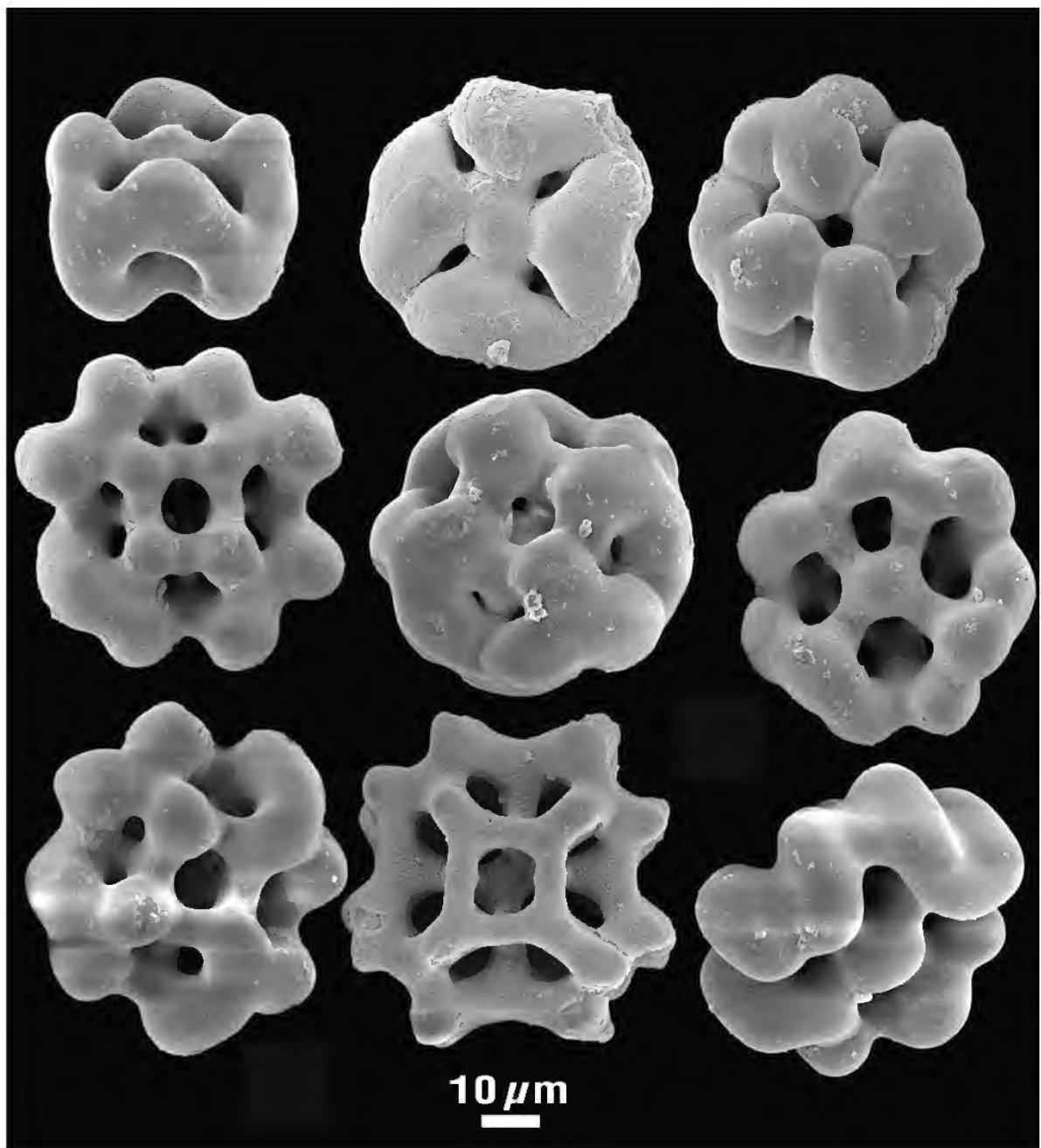


Figure 10. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina coriacea* (Hutton, 1872) from Cook Strait, New Zealand (NIWA 70954).

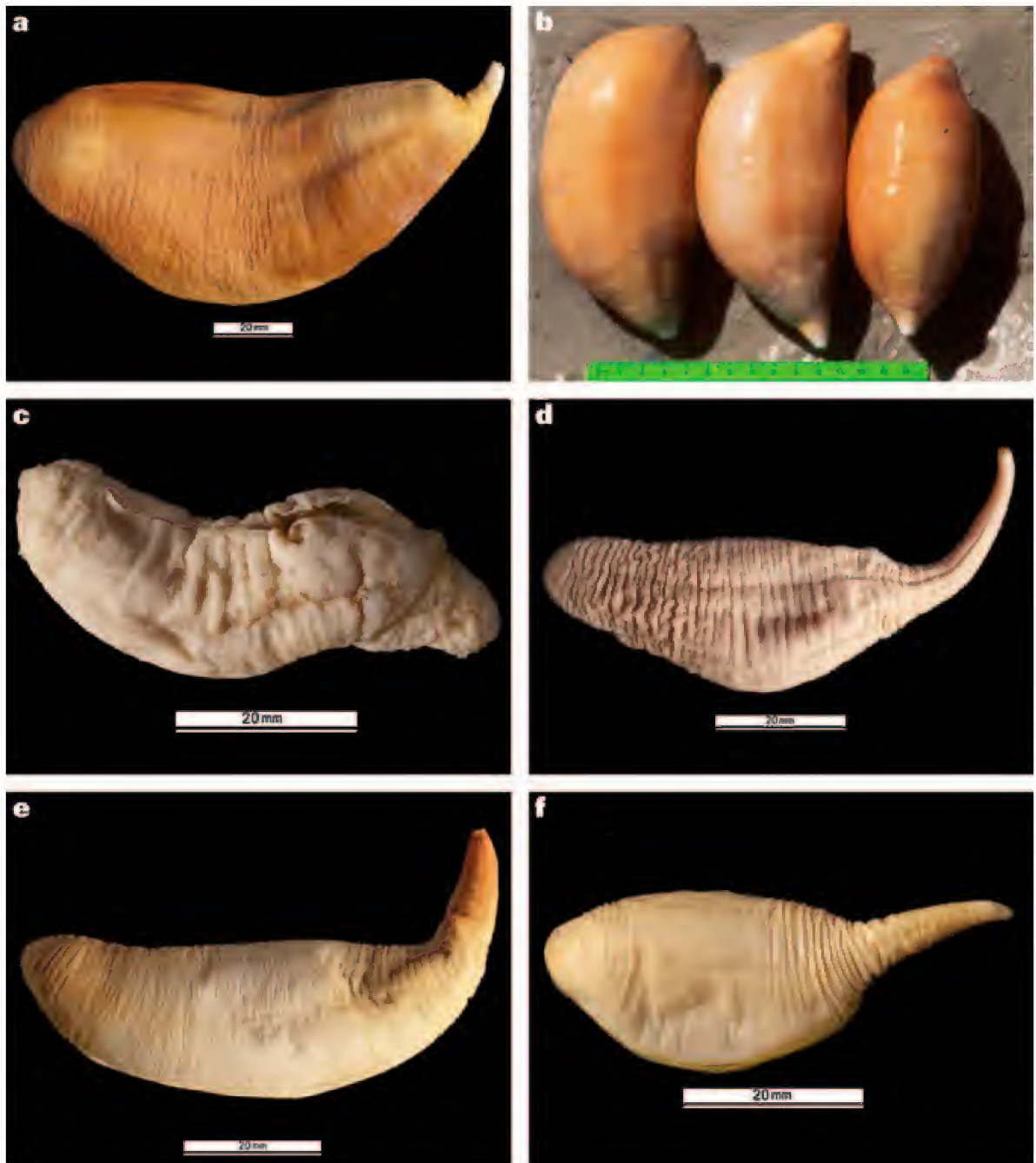


Figure 11. Photos of preserved specimens of species of *Paracaudina* (a, c–f): a, *P. cuprea* O'Loughlin and Barmos sp. nov. holotype (NMV F157396); b, photo of live specimens of *P. cuprea* including holotype (photo by P. Vafiadis); c, *P. keablei* O'Loughlin and Barmos sp. nov. holotype (AM J13579); d, *P. luticola* Hickman, 1962 (NMV F169342); e, *P. tetrapora* (H. L. Clark, 1914) (from Merricks, Westernport Bay, Victoria; NMV F76565); f, *P. tetrapora* (H. L. Clark, 1914) (from off Glenelg, South Australia; AM J24918).

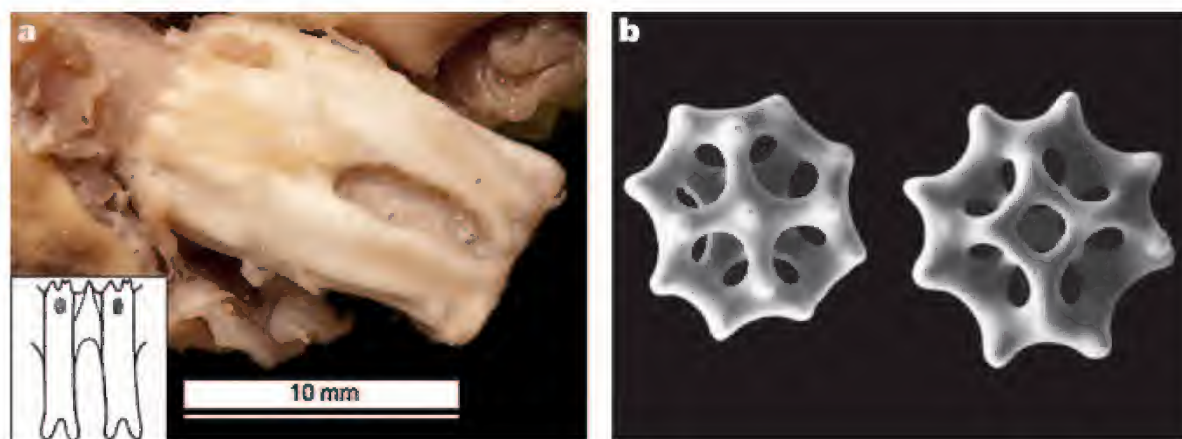


Figure 12. a, Calcareous ring of a specimen of *Paracaudina cuprea* O'Loughlin and Barmos sp. nov. from Portland Bay, Victoria (NMV F174890) (insert with drawing of two radial plates and one interradial plate typical of *Paracaudina* species); b, SEM images of ossicles from a specimen of *Paracaudina chilensis obesacauda* (H. L. Clark, 1908), judged here to be typical of *Paracaudina chilensis* (Müller, 1850) (copied from Pawson et al. 2001).

Paracaudina australis (Semper, 1868)

Figures 1b, 3, 4

Molpadia australis Semper, 1868: 233–234, 268, pl. 39 fig 14.—Théel, 1886: 55.

Caudina chilensis.—H. L. Clark, 1908: 175–176. (part non *Molpadia chilensis* Müller, 1850).

Pseudocaudina australis.—Heding, 1931: 283.

Paracaudina australis.—Heding, 1932: 455.—Heding, 1933: 127–142, pl. 6 figs 5–7, pl. 7 figs 8–9, pl. 8 fig. 6.—H. L. Clark, 1935: 267–284.—H. L. Clark, 1946: 45 (part).—A. M. Clark and Rowe, 1971: 193.—Pawson, 1977: 119 (part).—Rowe, 1982: 472 (part), fig. 10.35b.—Cannon and Silver, 1986: 40, figs 8f, 10f.—Rowe and Gates, 1995: 264 (part).

Material examined. Queensland, Moreton Bay, Stradbroke Island, Dunwich, half buried on sandbar, 2 Dec 1978, AM J13583 (1); Port Denison District, AM J4145 (5).

Diagnosis. *Paracaudina* species up to 135 mm long, up to 35 mm diameter (preserved); thin, pliable, soft to firm smooth body wall; colour translucent pink to white live, off-white to pale brown preserved, lacking yellow colouration, at most slight yellowing anteriorly; posterior body with caudal taper to narrow rounded end, sometimes short tail; mid-body ossicles predominantly plates with bluntly spinous margin and surface, smooth plates, rods in deeper body wall; ossicles not thick buttons; spinous plates irregular, pointed marginal projections, surface knobs / blunt spines frequently joined by rods creating secondary layering, rods sometimes bridging a large central perforation as single rod or tripod or cross, rare *chilensis*-like plates with large central perforation bridged by box on one side and cross on the other side, up to 12 perforations, spinous plates up to 56 μm long; smooth plates irregular, up to 12 perforations, margin smooth, lacking marginal and surface spines and knobs, smooth plates up to 48 μm long; rods sparse, irregular, variably straight, bent, Y-shaped, C-shaped, J-shaped, some

with node, rods frequently 24 μm long, up to 48 μm long.

Type locality. Rockhampton, Queensland.

Distribution. Northern Australia, Queensland, south-east coast; Singapore (?).

Remarks. *Paracaudina australis* (Semper, 1868) is distinguished diagnostically by having in the body wall both irregular rods and spinous perforated plates with secondary layering, a body form with tapered caudal end but not long discrete tail, and an absence of distinct yellow or reddish-yellow colour. H. L. Clark 1908 included *Paracaudina australis* in his synonymy of *Caudina chilensis*, but subsequently (1935, 1946) rejected his own synonymy. Southern Australian specimens judged to be *Paracaudina australis* by H. L. Clark 1946, Rowe 1982 and Rowe and Gates 1995 are our new species *Paracaudina cuprea* O'Loughlin and Barmos (below). Mortensen 1925 based his discussion of *Paracaudina australis* on SAM specimens. Based on Mortensen's figures we judge that these specimens were our new species *Paracaudina cuprea* O'Loughlin and Barmos (below). We note that Heding 1933 did not indicate what specimens he used to illustrate ossicles of *Paracaudina australis*.

David Lane (pers. comm. by Ria Tan) identified the common "See-through sea cucumber" in Singapore waters as *Paracaudina australis*. Ria Tan (pers. comm.) has observed the species only on the estuarine northern shores of Singapore near the mouth of the Johor River, floating or partly buried on sand bars near seagrass meadows, as shallow as the intertidal zone at low spring tide. We have to date not been able to confirm the determination as *Paracaudina australis*.

Paracaudina bacillis O'Loughlin and Barmos sp. nov.

Figures 5a–f, 6a–c

Paracaudina sp. Rowe, 1982: 470, fig. 10.34c.

Paracaudina australis.—Gowlett–Holmes, 2008: 263.—Saunders, 2009: 99, fig. 5.19. (non *Molpadia australis* Semper, 1868)

Material examined. Holotype. Victoria, Westernport Bay, Phillip Island, Ventnor, McHaffie Point, MRG, 16 Feb 2008, NMV F151853.

Paratypes. Westernport Bay, San Remo, Griffith Point, 2 Jan 1999, NMV F89700 (1); Merricks beach, 5 Nov 1967, NMV F45254 (1); 27 Jul 1969, NMV F45240 (1); 4 Jun 2011, NMV F174893 (1); 10 Jun 2011, NMV F174894 (1); Shoreham, 26 Aug 1978, NMV F76071 (2); 30 Mar 1902, NMV F173250 (1) (removed from Shoreham lot 60669–71 / H19 (3) examined in part by Joshua 1914).

Other material. Victoria, Westernport Bay, Crawfish Rock, 12 m, 13 Oct 1968, NMV F169343 (1); Somers, 28 Sep 1968, NMV F45273 (1); Port Phillip Bay, Brighton beach, NMV F45020 (1); Rosebud beach, NMV F173247 (1); Rye pier, 6 Apr 2011, NMV F173272 (1); Blairgowrie Marina, 5 m, 18 Jun 2011 (photo J. Finn, NMV); Tootgarook beach, 20 Jun 2011, NMV F174896 (1). South Australia, Yorke Peninsula, Browns Beach, SAM K2493 (6); Edithburgh, sand, 3–4 m, 12 May 1999, SAM K2486 (1); 2–3 m, 11 Jun 2005, SAM K2487 (1); sand, low tide, 26 Oct 2007 SAM K2490 (1); 8 Nov 2003, SAM K2491 (1). Western Australia, east of Duke of Orleans Bay, Mininup beach after storm, Nov 1990, WAM Z31888 (1); Albany, 5 Dec 1983, WAM Z31881 (1).

Diagnosis. *Paracaudina* species up to 180 mm total length, up 55 mm diameter, caudal taper 45 mm long (SAM K2491, preserved); thin, parchment-like to soft leathery body wall (preserved); live colour off-white, preserved colour off-white to pale yellow or brown; posterior body with caudal taper to narrow rounded end, sometimes short discrete tail, lacking a discrete long thin tail; body wall ossicles small irregular rods only, straight, bent, wavy, J-shaped, sometimes with nodes, rarely with short branches, up to 64 μ m long.

Type locality. Victoria, Westernport Bay, Phillip Island, Ventnor, McHaffie Point.

Distribution. Victoria (Westernport Bay, Port Phillip Bay), South Australia Gulfs, Eyre Peninsula, to southern Western Australia (Albany); 0–145 m (Rowe 1982); 0–230 m (Gowlett–Holmes 2008).

Etymology. From the Latin *baculus* (rod), and its diminutive *bacillus*, referring to the very small rod ossicles only in the body wall.

Remarks. *Paracaudina bacillis* O'Loughlin and Barmos sp. nov. is distinguished diagnostically amongst *Paracaudina* species by having only small irregular rod ossicles in the body wall. Rods of similar form occur also in *Paracaudina australis* (Semper, 1868), a species that also has irregular marginally spinous perforated plate ossicles in the body wall. Rowe 1982 recognised this “undescribed form” from Port Phillip Bay and southern Western Australia, and illustrated (fig. 10.34c) the diagnostically characteristic minute irregular rod ossicles from the body wall. Gowlett–Holmes 2008 illustrated and described a species from southern Australia as *Paracaudina australis* that has the body form, size up to 20 cm long, and off-white colour of *Paracaudina bacillis* O'Loughlin and Barmos sp. nov. Gowlett–Holmes 2008 described the habit as “usually completely buried 5–10 cm below the sediment surface; moves slowly through the sand feeding on detritus, leaving a broad

furrow-like trail”. Saunders 2009 also illustrated a specimen as *P. australis* at Coffin Bay on the Eyre Peninsula that we judge to be *P. bacillis* based on size and form and colour. Joshua 1914 referred two specimens from Westernport Bay and “Mordialloc” (Port Phillip Bay) to *Caudina chilensis* (Müller). We found these two specimens with a third specimen in lot H19 / 60669–71 / NMV F45019, and assigned (below) the two referred to by Joshua 1914 to the new species *Paracaudina cuprea* O'Loughlin and Barmos (F169344) and *Paracaudina tetrapora* (H. L. Clark, 1914) (F45019, original registration). The label indicated all three specimens were collected by J. A. Kershaw at Shoreham. We judge that Joshua's reference to “Mordialloc” was a mistake. We found no specimens from Mordialloc in the NMV collection. The third specimen in the lot, not commented on in Joshua 1914, is the third new species (above) *Paracaudina bacillis* O'Loughlin and Barmos (F173250).

Paracaudina chilensis (Müller, 1850)

Figures 1c, 7, 8, 12b

Molpadia chilensis Müller, 1850: 139.—Müller, 1854: pl. 6 fig. 14, pl. 9 fig. 1.—Semper, 1868: 233.—Théel, 1886: 55.

Microdactyla caudata Sluiter, 1880: 348–351, pl. 6 fig. 1, pl. 7 figs 1–6.

Caudina ransonnetii Marenzeller, 1881: 126–127, pl. 4 figs 5, 5A.—Ludwig, 1883: 158–159.—Lampert, 1885: 210.—Théel, 1886: 54.—Ludwig, 1891: 354.—Mitsukuri, 1912: 261–262, pl. 8 fig. 76.

Caudina caudata.—Ludwig, 1883: 159. (synonymy with *Caudina chilensis* (Müller) by H. L. Clark 1908)

Caudina coriacea.—Théel, 1886: 47, pl. 3 fig 4a–c. (non *Caudina coriacea* Hutton, 1872)

Caudina rugosa R. Perrier, 1904: 16.—R. Perrier, 1905: pl. 4 figs 10–12. (synonymy with *Caudina chilensis* (Müller) by H. L. Clark 1908)

Caudina pigmentosa Perrier, 1904: 16–17.—Perrier, 1905: pl. 4 figs 1–9. (synonymy by H. L. Clark 1935)

Caudina contractacauda H. L. Clark, 1908: 38–39, 173, 177, 178, pl. 9 figs 9–13. (synonymy by H. L. Clark 1935)

Caudina chilensis.—H. L. Clark, 1908: 173, 175–176.—Hozawa, 1928: 361–378, pls 14–17.—Ohshima, 1929: 39–45.

Pseudocaudina chilensis.—Heding, 1931: 283.

Pseudocaudina ransonnetii.—Heding, 1931: 283.

Paracaudina chilensis.—Heding, 1933: 127–142, pls 5–8.—H. L. Clark, 1935: 267–284.—Deichmann, 1938: 383–384, fig. 15.—Pawson, 1969: 139–140.—A. M. Clark and Rowe, 1971: 184–185.—Pawson, 1977: 119 (part).—Cannon and Silver, 1986: 40.—Rowe and Gates, 1995: 264.—Liao and Clark, A. M., 1995: 518–519, fig. 316.—Lane et al., 2000: 491.

Paracaudina ransonnetii.—Heding, 1933: 455.—Djakonov et al., 1958: 377.

Paracaudina chilensis var. *ransonnetii* H. L. Clark, 1935: 281.—H. L. Clark, 1938: 540–541.—H. L. Clark, 1946: 444.—A. M. Clark and Rowe, 1971: 194–195, fig. 96a. (synonymy by Liao and Pawson 1992)

Material examined. Western Australia, Roebuck Bay, Broome, Sep 1929, from H. L. Clark collection, AM J6435 (1); Eighty Mile Beach, 19°20'00"S 121°21'00"E, Annabim Expedition 1999, mudflat, WAM Z5637 (1); WAM Z5638 (2); WAM Z5639 (1); WAM Z5640 (1); WAM Z5641 (1); WAM Z5642 (1); WAM Z5653 (1); WAM Z5654 (1); WAM Z5655 (2 tails). New South Wales, Twofold Bay, Nullica Bay, 9.1 m, 22 Feb 1985 AM J19908 (one 3 mm fragment). New Zealand, South

Island, Tasman Bay, 41.17°S 173.17°E, 0 m, 24 Jan 1972, NIWA 70956 (2).

Diagnosis. *Paracaudina* species up to 150 mm total length, diameter up to 20 mm, caudal taper and long discrete tail 80 mm long; posterior body with discrete long thin tail, up to more than half the length of the body; body firm thin leathery to parchment-like, finely wrinkled, variably transversely creased (preserved), live colour off-white with slight purple colouration (H. L. Clark 1938; Liao and A. M. Clark 1995), preserved colour pale grey to pink-grey; mid-body ossicles predominantly octagonal plates with large central perforation bridged by basal box with 4 supporting arms on one side and cross with 4 supporting arms on the upper side, surface knobbed, margin with 8 bluntly pointed projections, plates up to 56 µm across.

Type locality. Chile.

Distribution. Circum-Pacific, including northwest Australia and New Zealand; to 1000 m (Pawson 1963).

Remarks. Ludwig 1883, Théel 1886, Heding 1931, 1933, and Djakonov et al. 1958 judged the Chinese / Japanese species *Paracaudina ransonnetii* (Marenzeller, 1881) to be a discrete species. Type locality is Yantai (Cheefoo) on the Yellow Sea. H. L. Clark 1935, 1938, 1946 (based on northern Australia material) and A. M. Clark and Rowe 1971 considered the species to be a variety of *Paracaudina chilensis* (Müller, 1850). H. L. Clark 1908, Hozawa 1928, Ohshima 1929, Pawson and Liao 1992, Rowe and Gates 1995, and Liao and Clark A. M. 1995 considered *Paracaudina ransonnetii* to be a junior synonym of *Paracaudina chilensis*. We agree with this synonymy. We judge that some north-western Australian material is *Paracaudina chilensis*, and that some north-eastern Australia material (from the Gulf of Carpentaria and Moreton Bay) is a new species *Paracaudina keablei* O'Loughlin and Barmos that we describe below.

Below we raise the New Zealand species *Paracaudina coriacea* (Hutton, 1872) out of synonymy with the Chilean species *Paracaudina chilensis* (Müller, 1850). Théel 1886 was prompted to refer New Zealand specimens to *Caudina ransonnetii* Marenzeller, 1881 but finally referred them to *Caudina coriacea* (Hutton, 1872). But the ossicles illustrated by Théel 1886 are the predominant ossicle form found in *Paracaudina chilensis*. We examined two small New Zealand specimens (NIWA 70956) from the shallows of Tasman Bay and found the ossicles to be those of *Paracaudina chilensis* (fig. 8). We dismissed our consideration that this ossicle form might be a juvenile developmental stage of *Paracaudina coriacea* on the grounds that Hozawa 1928 found no such significant development changes in his study of *Paracaudina chilensis* at Asamushi. Both *Paracaudina chilensis* (Müller) and *Paracaudina coriacea* (Hutton) occur in New Zealand waters. We note that the distal tail of the specimen of *Paracaudina chilensis* WAM Z5638 is not very thin (fig. 1c), while the distal tails of the two specimens of *Paracaudina coriacea* NIWA 70955 and AM J12290 are both very thin (figs 1d, e).

We also note that some, but not the predominant, ossicles from specimens judged to be *Paracaudina chilensis* from northwest Australia are similar to the ossicles illustrated for

the single type specimen of *Paracaudina delicata* Pawson and Liao, 1992 taken in the Gulf of Tonkin. And some, but not the predominant, ossicles are similar to those in the new species *Paracaudina keablei* O'Loughlin and Barmos (below).

Paracaudina coriacea (Hutton, 1872)

Figures 1d–f, 9, 10

Molpadia coriacea Hutton, 1872: 17.—Hutton, 1879: 307.—Lampert, 1885: 208–209.

Echinostoma (?) *coriacea*. —Hutton, 1879: 307. (synonymy with *Caudina coriacea* (Hutton) by Théel 1886)

Caudina meridionalis Bell, 1883: 58–59, pl. 15 fig. 1.—Lampert, 1885: 210–211. (synonymy with *Caudina coriacea* (Hutton) by Théel 1886)

Caudina coriacea.—Théel, 1886: 54–55.—Dendy, 1897: 28–32, pl. 3 figs 9–18.—Dendy, 1898: 456–464, pl. 29.—Farquhar, 1898: 324.—Ludwig, 1898: 63–64.—Dendy and Hindle, 1907: 95, 108–110, fig. B.—Mortensen, 1925: 364–366, figs 46b, 47b. (synonymy with *Caudina chilensis* (Müller) by H. L. Clark 1908)

Caudina coriacea var. *brevicauda* R. Perrier, 1905: 121–123, fig. N. (synonymy with *Caudina coriacea* by Dendy and Hindle 1907; with *Paracaudina chilensis* var. *coriacea* by H. L. Clark 1935)

Caudina pulchella R. Perrier, 1905: 117–120, pl. 5 figs 14–17. (synonymy with *Caudina coriacea* by Dendy and Hindle 1907; with *Paracaudina chilensis* var. *coriacea* by H. L. Clark 1935)

Caudina chilensis.—Benham, 1909: 110. (non *Paracaudina chilensis* (Müller, 1850))

Paracaudina chilensis var. *coriacea*.—H. L. Clark, 1935: 267–284.

Paracaudina chilensis.—Pawson, 1963: 18–21, pl. 4.—Pawson, 1965: 14.—Pawson, 1970: 49–50, pl. 2 fig. 2.—Pawson, 1977: 119 (part).—Mah et al., 2009: 382, 398, fig. p. 383. (non *Paracaudina chilensis* (Müller, 1850))

Material examined. New Zealand, Cook Strait, 61 m, 26 May 1975, NIWA 70954 (1); Cook Strait, 18 m, 15 Dec 1983, NIWA 70955 (1); South Island, west coast, Arawhata River mouth, washed onto spit, 8 Jul 1969, AM J12290 (3).

Diagnosis. *Paracaudina* species up to 172 mm total length, up to 28 mm diameter, caudal taper and narrow tail 102 mm long (NIWA 70954); discrete thin tail, frequently longer than main body; body wall parchment-like, smooth to wrinkled, frequently with transverse creasing, preserved colour off-white with patches of yellowish-red (rusty) colouration in largest specimens; mid-body ossicles predominantly thick, button-like, octagonal, with central perforation bridged by a box basally and cross on the upper side, perforations small, margin predominantly rounded and lacking projecting knobs and bluntly pointed projections, surface variably knobbed or with short thick spines, ossicles typically 64 µm, up to 80 µm long.

Distribution. New Zealand; 0–61 m.

Remarks. In erecting the species *Caudina meridionalis* (junior synonym of *P. coriacea*) for two specimens from New Zealand waters, Bell 1883 noted that in comparison with *Caudina ransonnetii* Marenzeller, 1881 (junior synonym of *P. chilensis*) the ossicles were “stout”, the perforations “small”, and the marginal projections not as distinct. We agree that these are a significant diagnostic difference between the predominant

ossicle forms of *Paracaudina coriacea* and *Paracaudina chilensis*. We raise *Paracaudina coriacea* (Hutton, 1872) out of synonymy with *Paracaudina chilensis* (Müller, 1850).

Perrier 1905 illustrated (pl. 5 figs 16, 17) what he considered to be the predominant ossicle form in his *Caudina pulchella* from New Zealand. Perrier 1905 also illustrated two ossicles (fig. N) for his New Zealand variety *Caudina coriacea* var. *brevicauda*. In both cases these are the thick ossicles with rounded margin and small perforations that we have found and illustrated as the predominant ossicles in New Zealand specimens of *Paracaudina coriacea* examined in this work. This form of ossicle was illustrated for New Zealand specimens by Dendy 1897, Mortensen 1925, Heding 1933 (pl. 6 figs 10–13, New Brighton, Christchurch, specimen), and Pawson 1963 (cups from adult specimen). These are the predominant ossicles of *Paracaudina coriacea* (Hutton).

Perrier 1905 illustrated (pl. 4 figs 11, 12) what he considered to be the predominant ossicle form in his *Caudina rugosa* from Cape Horn, and they are the ossicles of medium thickness with prominent blunt marginal projections that we have found in the Australian and New Zealand specimens of *Paracaudina chilensis* (Müller) examined in this work. This form of ossicle was illustrated by Müller 1854, Marenzeller 1881, Clark 1908, Hozawa 1928, Heding 1933 (pl. 6 figs 1–4, type), Pawson and Liao 1992, Liao and Clark 1995 and Pawson et al. 2001 for material falling within the synonymy of *Paracaudina chilensis*.

We note that Heding 1933 (pl. 6 figs 8–9) illustrated ossicles from a New Zealand specimen from Tiritiri Matangi (north of Auckland) that we judge to be typical of *Paracaudina chilensis*. If this was the predominant ossicle form the specimen was *Paracaudina chilensis*.

Our New Zealand colleagues were unsuccessful in attempting to find the type material for *Molpadia coriacea* Hutton, 1872.

Paracaudina cuprea O'Loughlin and Barmos sp. nov.

Figures 11a, b, 12a, 13

Caudina chilensis.—Joshua, 1914: 6 (part).—Joshua and Creed 1915: 21–22 (part). (non *Molpadia chilensis* Müller, 1850)

Caudina australis.—Mortensen, 1925: 364–367, figs 46c, 47a. (non *Molpadia australis* Semper, 1868)

Paracaudina australis.—Hickman, 1962: 63–64, figs 106–130, pl. 2 fig. 9.—Rowe, 1982: 472 (part), pl. 32.3.—Rowe and Gates, 1995: 264 (part). (non *Molpadia australis* Semper, 1868)

Material examined. Holotype. Victoria, Corner Inlet, Sunday Island, mudflat, MRG, 15 Mar 2004, NMV F157396.

Paratypes. Corner Inlet, Port Welshpool, in sediment, MRG, 5 Mar 2010, NMV F169322 (2).

Other material. Victoria, Seaspray, 8 Mar 1977, AM J10610 (1); Westernport Bay, San Remo, 2 Apr 1972, NMV F169346 (1); Shoreham, 30 Mar 1902, NMV F169344 (1) (removed from Shoreham lot 60669–71 / H19 (3) examined in part by Joshua 1914); Portland Bay, 27–35 m, 29 Aug 1975, NMV F76073 (1); NMV F174890 (1). Tasmania, Seven-mile Beach, 13 Aug 1956, AM J7195 (1); Roches Beach, 6 Mar 1974, AM J8437 (4). South Australia, 24 Jun 1924, SAM K2504 (1); St Vincent Gulf, mixed localities, Aug 1886, SAM K1381 (13); Port Stanvac, dredged 16 m, 6 Feb 1991, SAM K2495 (12); SAM

K2498 (1); Apr 1991, 17 m, SAM K2503 (1); Brighton Beach, 3 Jul ? 1916, SAM K2506 (2); Port Lincoln, 5 m, 22 Aug 1975, SAM K2492 (1). Western Australia, AM J2341 (1; no additional data); AM J2342 (1; no additional data); Rottnest I., 146–155 m, 15 Aug 1962, WAM Z8977 (1); 139–145 m, 12 Aug 1962, WAM Z8979 (1); 183–188 m, 14 Aug 1962, WAM Z8981 (1); 146 m, 10 Aug 1962, WAM Z8985 (1).

Diagnosis. *Paracaudina* species up to 153 mm long (F169346, preserved), main body 144 mm long, width up to 55 mm, tail 9 mm long; cylindrical body sharply tapered at ends to pointed oral end, discrete short narrow caudal end / tail; thick, firm, leathery body wall, smooth, slight wrinkling at oral and anal ends, variable transverse creasing; live and preserved colour variably rusty, orange, copper, yellow, some off-white patches; oval yellow phosphatic bodies present, up to 40 µm long; mid-body ossicles irregular, variable, round to oval small plates, flat to slightly concave, margin and surface smooth or with pointed spines or knobs, knobs sometimes joined to create secondary layering, up to 12 irregular perforations, frequently with large central perforation and or lacking surrounding perforations, central perforation bridged by 1 or 3 or 4 arms, rarely *chilensis*-like and bridged by cross on one side and box on other side, ossicles up to about 60 µm long.

Type locality. Victoria, Corner Inlet, Sunday Island, intertidal sediments.

Distribution. Southern Australia, from eastern Victoria (Seaspray), south to Tasmania, and west to Rottnest Island (off Perth); 0–188 m.

Etymology. From the Latin *cupreus* (copper), referring to the coppery, rusty colour of live and preserved specimens

Remarks. The diagnostic characters that distinguish the new species *Paracaudina cuprea* O'Loughlin and Barmos are the distinctive body form with discrete, short narrow tail, the rusty and orange colour, absence of mid-body wall rods, and the predominance of irregular, perforated plate ossicles frequently with irregularly bridged central perforation and with blunt marginal and surface spines and knobs.

Joshua 1914 determined a 100 mm long specimen (seen here, F169344) from “Mordialloc” on Port Phillip Bay as *Caudina chilensis* (Müller), but reported that it tapered sharply posteriorly and could not be described as caudate. Colour was yellow, blotched with brownish pink. The cross in the ossicles was frequently lost by fusion with the disc. He was referring to a specimen of the new species *Paracaudina cuprea* O'Loughlin and Barmos. As discussed in the Remarks under *P. bacillis* (above) we judge from specimen labels that the specimen came from Shoreham on Westernport Bay, not “Mordialloc”. Although they determined specimens from South Australia as *Caudina chilensis* (Müller), Joshua and Creed 1915 described some of them as being up to 125 mm long, lacking the caudate character of the species, and yellow with patches of rusty red in colour. They were referring to specimens of the new species *Paracaudina cuprea*. Hickman 1962 also described and illustrated (as *P. australis*) the new species *Paracaudina cuprea*. Rowe 1982 (pl. 32.3) also illustrated this new species (as *P. australis*), and in describing the colour of southern Australian specimens as “rusty pink and brown” was referring

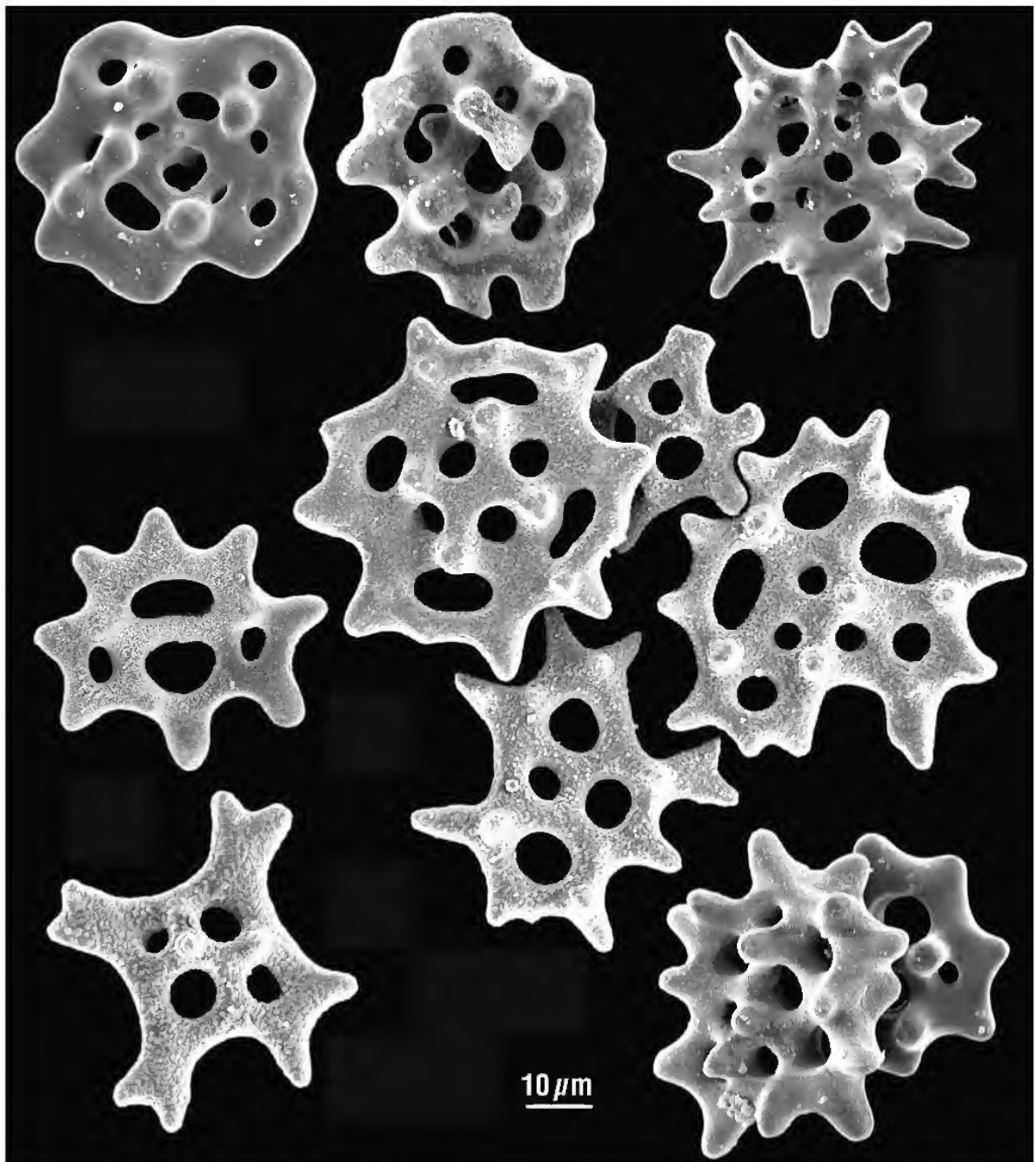


Figure 13. SEM images of ossicles from the mid-body wall of the holotype specimen of *Paracaudina cuprea* O'Loughlin and Barmos sp. nov. from Sunday Island, Corner Inlet, Victoria (NMV F157396).

to the new species *Paracaudina cuprea*. Mortensen 1925 based his discussion of *Paracaudina australis* on SAM specimens. Based on Mortensen's figures we judge that these specimens were our new species *Paracaudina cuprea*.

Paracaudina keablei O'Loughlin and Barmos sp. nov.

Figures 11c, 14

Material examined. Holotype. Queensland, Moreton Bay, Stradbroke Island, Dunwich, sandbar, H. Silver, 2 Dec 1978, AM J13579.

Other material. Queensland, Gulf of Carpentaria, SE corner, 17°24'55"S 140°42'35" E, 4.6 m, CSIRO Rama prawn survey trawl stn 555, 16 Jan 1964, AM J17085 (1); 17°30'15"S 140°40'10" E, 2.3 m, CSIRO Rama prawn survey trawl stn 494, 18 Dec 1963, AM J17051 (3).

Diagnosis. *Paracaudina* species up to 75 mm total length, diameter up to 18 mm, caudal taper and short discrete tail 25 mm long (preserved); body wall firm, not thin, smooth to wrinkled, partly transversely creased, slightly rugose, off-white (preserved); short caudal taper and discrete thin tail; no evidence of phosphatising; mid-body ossicles predominantly thin-walled octagonal plates with large central perforation, basal box with 4 supporting arms bridging one side of ossicle, cross with 4 supporting arms bridging outer side, short blunt spines only around marginal surface and on cross, not on box, lacking prominent marginal sub-digitiform projections and knobs, ossicles up to 70 µm across.

Type locality. Northeast Australia, Moreton Bay.

Distribution. Northeast Australia, Moreton Bay, Stradbroke Island, Gulf of Carpentaria; 0–5 m.

Etymology. Named for Dr Stephen Keable, Collection Manager, Marine Invertebrates (Natural Science Collections), Australian Museum, in appreciation of his prompt and gracious assistance with loans from the Australian Museum for this and other research projects.

Remarks. The holotype specimen of *Paracaudina keablei* O'Loughlin and Barmos sp. nov. is damaged, but the ossicles are in good condition. The ossicles in the additional material are somewhat eroded, but the predominant ossicle form is diagnostically distinguishable. Four *Paracaudina* Hedding species have a predominant ossicle form of octagonal plates with a basal box with four supporting arms bridging the ossicle on one side and a cross with four supporting arms bridging the ossicle on the opposite side. The predominant ossicle form in *Paracaudina chilensis* (Müller) is of moderate thickness with prominent knobs and sub-digitiform projections around the margin. The predominant ossicles in *Paracaudina coriacea* (Hutton) are thick buttons with rounded margin and small perforations. *Paracaudina keablei* sp. nov. is distinguished from both these species by having a predominant ossicle form of thin-walled plates with large perforations and lack of prominent marginal projections. The ossicles in *Paracaudina delicata* Pawson and Liao, 1992 are also thin-walled, but have numerous fine digitiform projections around the margin. *Paracaudina keablei* is further distinguished from the other three species mentioned here by having a short thin tail.

Paracaudina luticola Hickman, 1962

Figures 11d, 15

Caudina chilensis.—Joshua and Creed 1915: 21–22 (part) (non *Molpadia chilensis* Müller, 1850).

Paracaudina luticola Hickman, 1962: 65–66, figs 131–139.—Hickman, 1978: 32, figs 25–44, pl. 2.—Pawson, 1977: 119.—Rowe, 1982: 471, fig. 10.35a.—Rowe and Gates, 1995: 265.

Material examined. Syntypes. Tasmania, Derwent Estuary, Ralph's Bay, 13 m, 30 Jun 1959, AM J7205 (2).

Other material. Victoria, Shallow Inlet, mud/sand seagrass, intertidal, 2 Feb 1990, NMV F169342 (2); Wilson's Promontory, Waratah Bay, Sandy Point, 31 Mar 1969, NMV F76072 (1). South Australia, SAM K1379 (1); Aug 1886, SAM K1380 (1); St. Vincent Gulf, donated by SAM, NMV F45018 (3; labelled as determination by Joshua and Creed in 1915 as *Caudina chilensis*); St Vincent Gulf, mixed localities, Aug 1886, SAM K2484 (1); Adelaide Outer Harbour, Feb 1935, SAM K2505 (1); Port Stanvac, 6 Feb 1991, SAM K2499 (1); Henley Beach, SAM K2488 (1); Brighton to Semaphore, SAM K2494 (2); Largs Bay beach, 26 Aug 1971, SAM K2508 (1); Edithburgh, Sultana Point, sand bar, 8 Nov 2003, SAM K2489 (1); Sir Joseph Banks Group, Marum I., in *Posidonia*, 12 m, 11 Jan 1984, SAM K2497 (1); Port Lincoln, 22 Aug 1975, AM J9466 (1); Venus Bay, 1982, SAM K2500 (4); Edward Bay, N of Streaky Bay, 23 Oct 1986, SAM K2483 (1). Western Australia, Bremer Bay, near Albany, on beach after storm, 5 Aug 1984, WAM Z31887 (1).

Diagnosis. *Paracaudina* species up to 137 mm total length, up to 19 mm diameter, caudal taper and discrete thin tail 52 mm long (up to 160 mm long live, Hickman 1978); long thin discrete tail; body wall thin, firm, parchment-like, variably wrinkled and transversely creased, preserved colour off-white to faint pink to grey; ossicles variable in form, similar from mid-body and tail, predominantly thick crossed cups, oval in form, large central perforation, lacking peripheral perforations, about 10–12 projecting marginal knobs, fewer marginal surface knobs, central perforation spanned by discrete cross, each arm of cross with rounded knob-like end; ossicles never with bridging cross on one side and box on other side of central perforation; ossicles up to about 56 µm long.

Type locality. Tasmania, Derwent Estuary, Ralph's Bay, 13 m.

Distribution. Southern Australia; southern Tasmania, north to Shallow Inlet (east of Wilson's Promontory, Victoria), west to Streaky Bay (west side of Eyre Peninsula in South Australia) and Bremer Bay (near Albany in Western Australia); 0–13 m.

Remarks. Hickman 1962 erected this species for caudal part-specimens only, but subsequently (1978) described whole specimens from the type locality. Ossicle size and form do not vary for body wall tissues taken from the main body and tail. The predominant ossicle form of thick four-holed cups with marginal and surface knobs and discrete cross is diagnostically distinctive for *Paracaudina luticola* Hickman, 1962. Joshua and Creed 1915 determined specimens from South Australia to be *Caudina chilensis* (Müller) that showed a "very great variation". We judged above, from their description, that some of the larger specimens were *Paracaudina cuprea* O'Loughlin and Barmos. We judge here, from their description of "about 70 mm long, white colour, markedly caudate discrete tail about

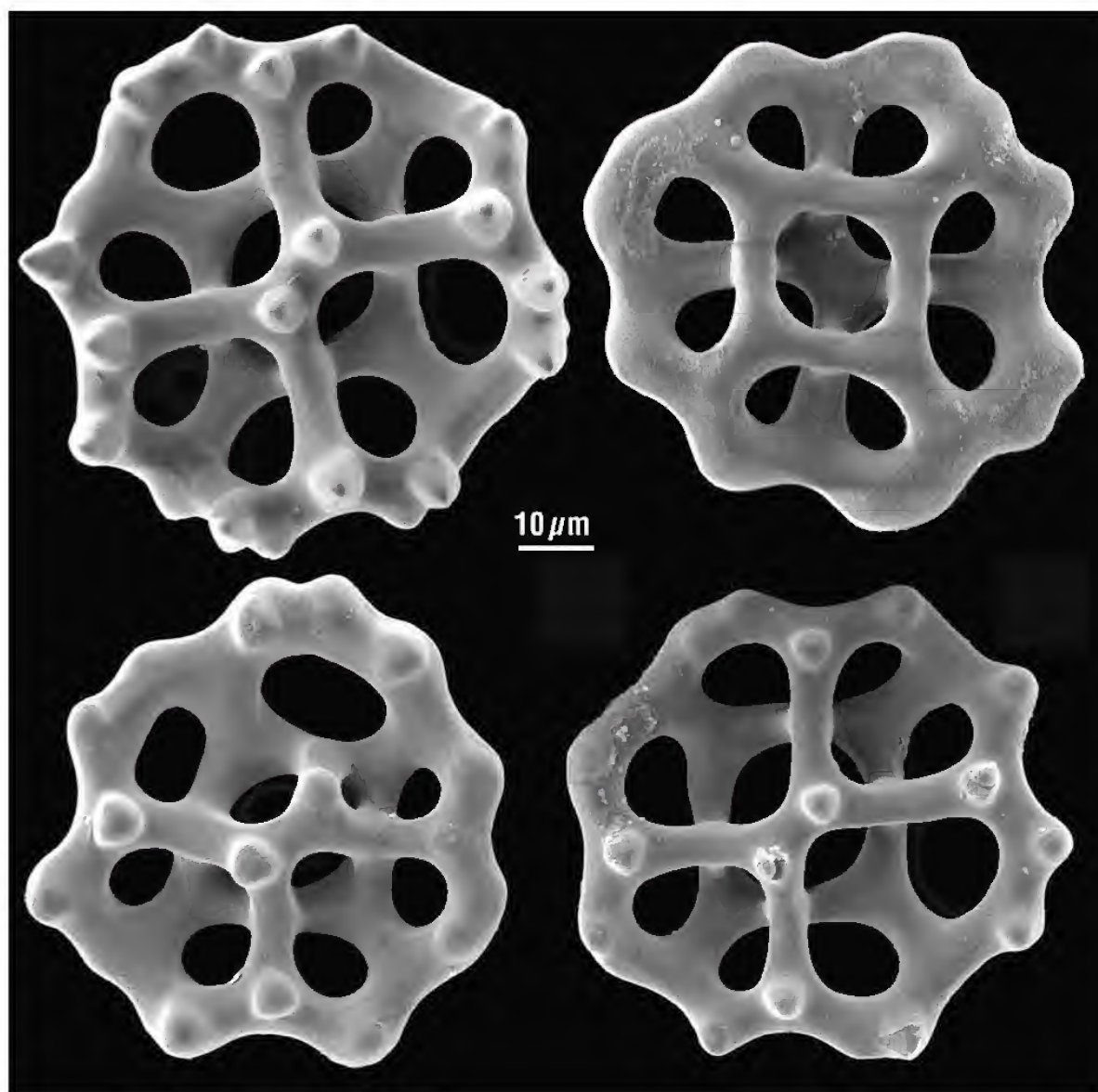


Figure 14. SEM images of ossicles from the mid-body wall of the holotype specimen of *Paracaudina keablei* O'Loughlin and Barmos sp. nov. from Dunwich, Stradbroke Island, Moreton Bay, Queensland (AM J13579).

half the length of the whole specimen", that some of the specimens were *Paracaudina luticola* Hickman.

***Paracaudina tetrapora* (H. L. Clark, 1914)**

Figures 11e, f, 16, 17

Caudina chilensis.—Joshua, 1914: 6 (part) (non *Molpadia chilensis* Müller, 1850).

Caudina tetrapora H. L. Clark, 1914: 170, fig. 1.

Paracaudina tetrapora.—H. L. Clark, 1935: 267–284.—H. L. Clark, 1938: 541.—H. L. Clark, 1946: 445.—Pawson, 1977: 119.—Rowe, 1982: 472.—Rowe and Gates, 1995: 265.

Material examined. Western Australia, Perth, Kwinana beach, Oct 1958, WAM Z31886 (1); South Cottesloe, 8 Nov 2008, WAM Z31883 (1). South Australia, Spencer Gulf, Sir Joseph Banks Group, Marum I., sand, 5 m, 8 Jan 1984, SAM K2496 (1); St. Vincent Gulf, North Haven to Largs Jetty, seagrass, 1 Dec 1980, SAM K2501 (1); Brighton Beach, 14 Feb 1975, SAM K2507 (2); off Glenelg, 10 m, 15 Feb 1969, AM

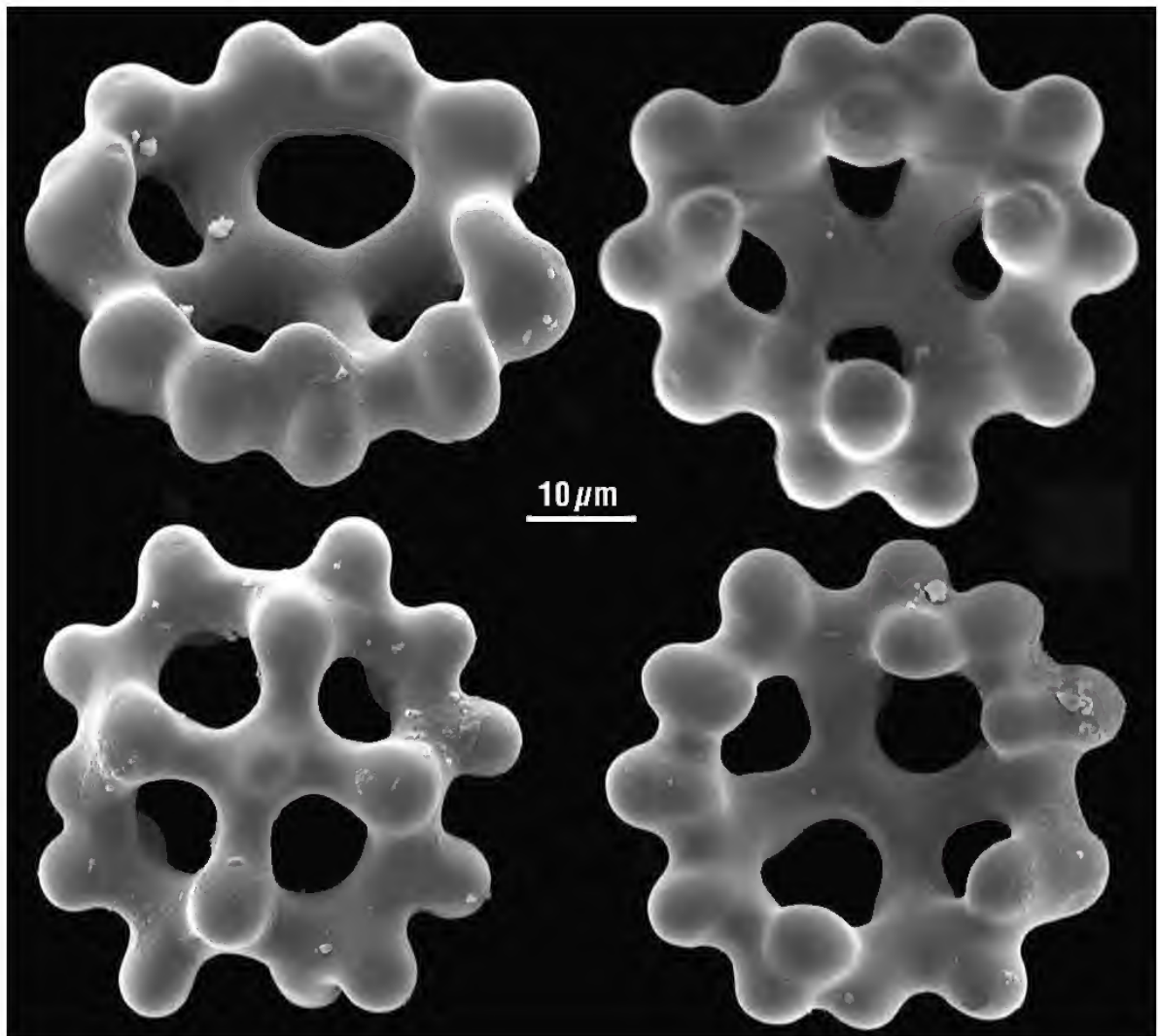


Figure 15. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina luticola* Hickman, 1962 from Sandy Point, Waratah Bay, Victoria (NMV F76072).

J24918 (1); mixed localities, Aug 1886, SAM K2485 (2). Victoria, Westernport Bay, Merricks, 29 Jan 1983, NMV F76565 (1); Flinders, beach, Jul 1967, NMV F45259 (1); Shoreham, 30 Mar 1902, NMV F45019 (remaining specimen from Shoreham lot 60669–71 / H19 (3) examined in part by Joshua 1914); Merricks, beach, Apr 1969, NMV F45274 (1).

Diagnosis. *Paracaudina* species up to 116 mm total length, up to 24 mm diameter, caudal taper and thin tail combined length 53 mm (preserved; WAM Z31886); firm leathery to parchment-like body wall with slight wrinkling; off-white to cream preserved colour, some yellow to yellowish-red colouration, some phosphatising with yellow colouration around eroding ossicles; posterior body with distinct long caudal taper to

narrow rounded end, sometimes tapering to a discrete long thin tail; mid-body ossicles predominantly 4-holed thick buttons, also thick perforated plates and bluntly spinous cups; 4-holed buttons irregularly oval to rectangular, some shallow concave, frequently 4 perforations with 2 large central and 2 small distal, variably thickened and marginally knobbed, up to 48 μm long; some thick irregularly oval to round perforated plates with up to 15 small perforations, margin and surface variably lumpy and knobbed and with blunt pointed projections, rare joining of knobs to create secondary layering, thickened plates up to 72 μm long, more evident in larger specimens; shallow cups with 4 perforations, long blunt thick marginal spines, marginal surface knobs, up to 72 μm long, more evident in larger

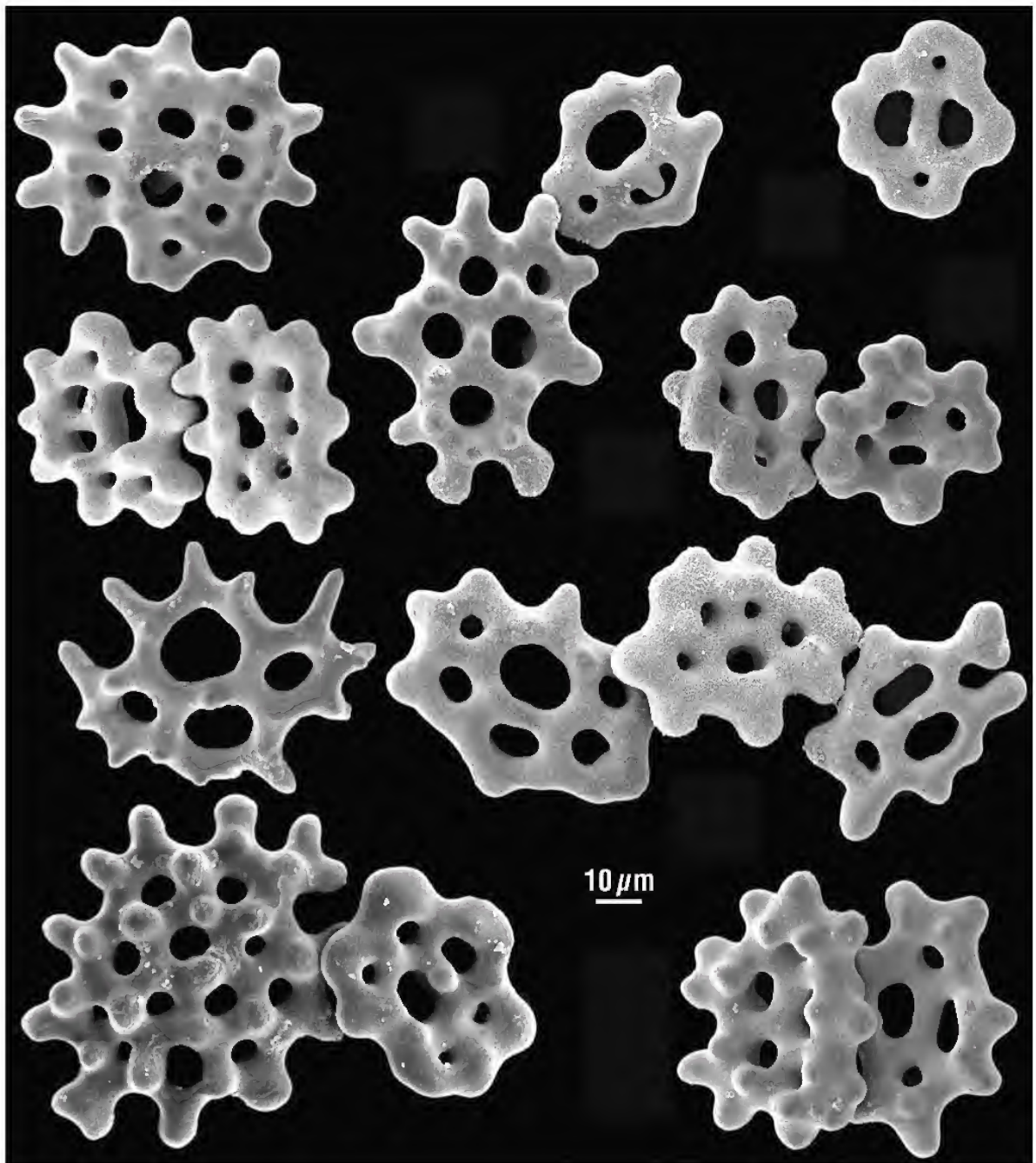


Figure 16. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina tetrapora* (H. L. Clark, 1914) from Merricks, Westernport Bay, Victoria (NMV F76565).

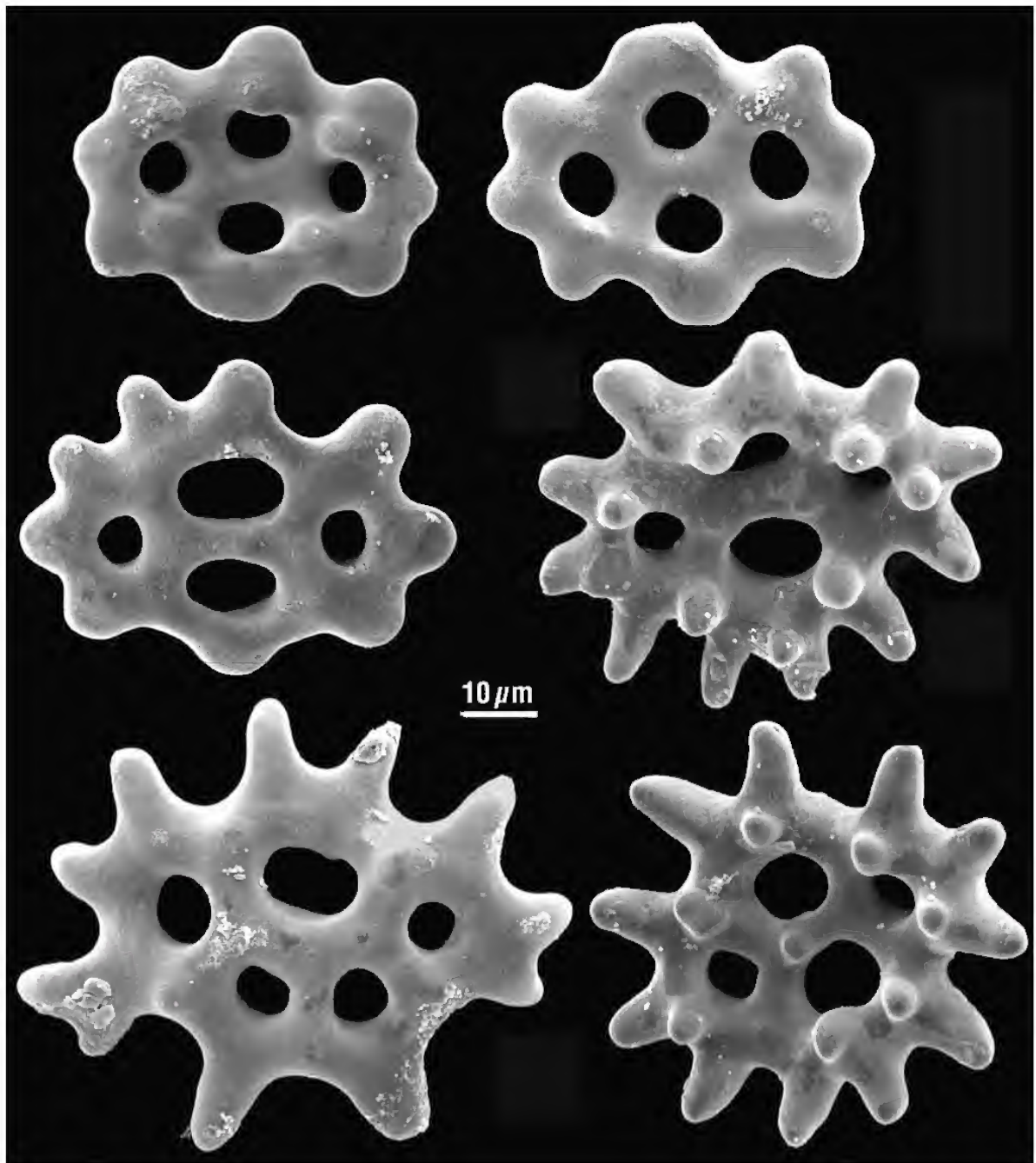


Figure 17. SEM images of ossicles from the mid-body wall of a specimen of *Paracaudina tetrapora* (H. L. Clark, 1914) from off Glenelg, St. Vincent Gulf, South Australia (AM J24918).

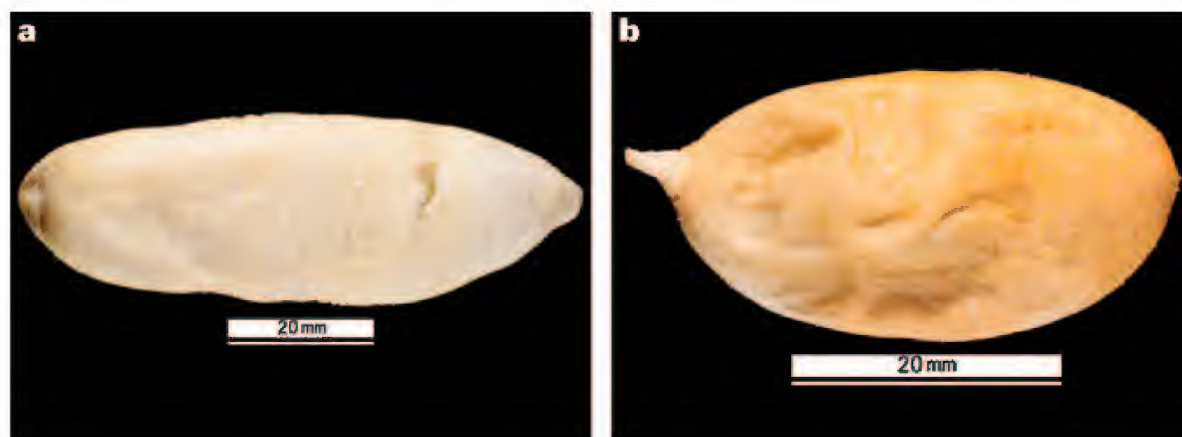


Figure 18. Photos of *Paracaudina tripoda* O'Loughlin and Barmos, sp. nov. (photos by L. Altoff, MRG). a, holotype from Queensland, east of Lady Elliot Island, 230 m (AM J24922); b, small paratype, north of Fraser Island, 137 m, (AM J11150 (7)).

specimens; ossicles never *chilensis*-like with central perforation with box and cross bridges.

Type locality. Western Australia, Perth, Cottesloe beach.

Distribution. Southern Australia, from Abrolhos Islands, Western Australia, to Westernport Bay, Victoria; to 10 m.

Remarks. *Paracaudina tetrapora* (H. L. Clark, 1914) is distinguished amongst Australian species of *Paracaudina* by having ossicles that are thick knobbed irregularly oval buttons with predominantly 2 large central and 2 distal smaller holes. Joshua 1914 reported two specimens from Victoria as *Caudina chilensis* (Müller). Details provided for the larger one (and confirmed here, NMV F169344) indicate that it was *Paracaudina cuprea* O'Loughlin and Barmos sp. nov. (above). The second specimen (seen here, NMV F45019) was *Paracaudina tetrapora* (H. L. Clark). Yellow body wall colouration with phosphatising of ossicles and phosphatic body wall residues is evident in larger specimens. In the largest specimen (SAM K2507) there is dark red phosphatising of the calcareous ring, and the reddish-brown colouration of the polian vesicle is presumed to be due to phosphatising.

***Paracaudina tripoda* O'Loughlin and Barmos sp. nov.**

Figures 18, 19

Material examined. Holotype. Queensland, east of Lady Elliot Island, 24°07'S 152°52'E, 230 m, 7 Jul 1984, AM J24922.

Paratypes. Type locality and date, AM J18814 (3); east of Lady Elliot Island, 24°04'S 152°48'E, 192 m, 7 Jul 1984, AM J18813 (1); north of Fraser Island, 24°23'S 153°17'30"E, 137 m, 15 Dec 1977, AM J11150 (7).

Diagnosis. *Paracaudina* species up to 75 mm total length, diameter up to 27 mm; oral and caudal tapers, lacking long thin tail, sometimes short discrete tail; body wall firm, leathery, slightly rugose; small preserved specimens reddish-yellow (rusty), larger specimens off-white; reddish-yellow pigment

may be present; mid-body with abundant irregularly round to oval, thick button-like ossicles, some slightly concave, up to 64 μ m long; majority of ossicles with rounded edge, short thick surface spines, ossicles frequently with large central perforation with tripod or single rod or cross bridge, up to 11 variably sized perforations; many *australis*-like plates with horizontal marginal projections; some *chilensis*-like plates with bridging box and cross over central perforation, some with bridging tripod; rare *ambigua*-like mid-body plate ossicles with 2–4 perforations, up to 32 μ m long.

Type locality. Northeast Australia, Queensland, E of Lady Elliot Island, 230 m.

Distribution. Northeast Australia, off Lady Elliot and Fraser Islands; 137–230 m.

Etymology. From the Greek *trion* (three) and *podos* (foot), referring to the frequency of a tripod bridge over the central perforation in the ossicles.

Remarks. The holotype specimen of *Paracaudina tripoda* O'Loughlin and Barmos sp. nov. is damaged, but the ossicles are in good condition and the body form is evident. Three *Paracaudina* Heding, 1932 species lack a long thin tail and have irregular small plate or button ossicles in the mid-body wall. In two of these species, *Paracaudina australis* (Semper, 1868) and *Paracaudina cuprea* O'Loughlin and Barmos sp. nov., the predominant ossicles from the mid-body are plates with lateral rounded marginal spines and surface spines and knobs. In the new species *Paracaudina tripoda* O'Loughlin and Barmos the predominant ossicles lack lateral rounded marginal spines, and have surface spines. *Paracaudina australis* specimens show rare slight yellowing, and have rods in the mid-body wall. *Paracaudina cuprea* specimens show strong reddish-yellow colouration with increasing size. *Paracaudina tripoda* specimens show decreasing reddish-yellow colouration with increasing size.

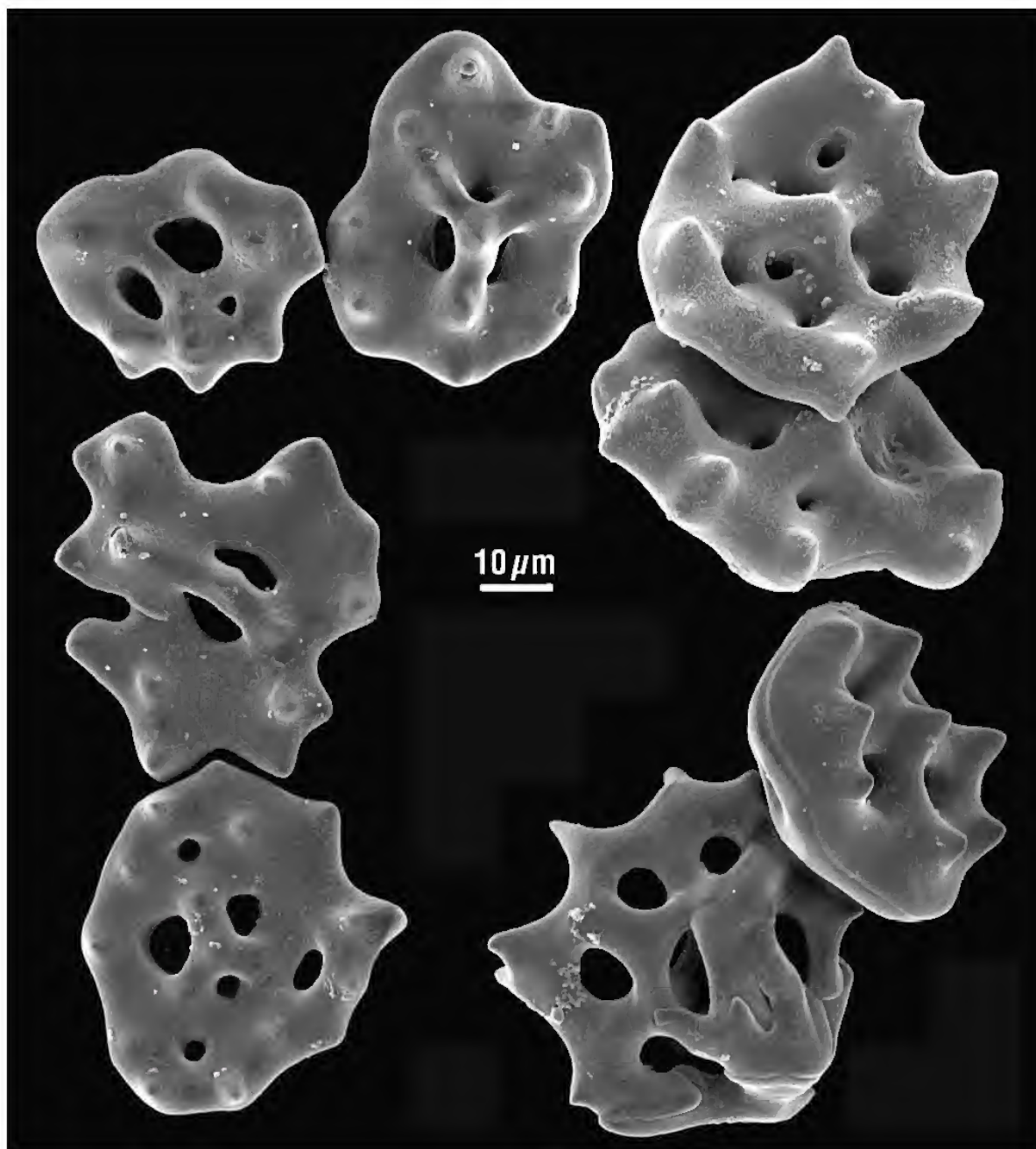


Figure 19. SEM images of ossicles from the mid-body wall of the holotype of *Paracaudina tripoda* O'Loughlin and Barmos sp. nov. (AM J24922).

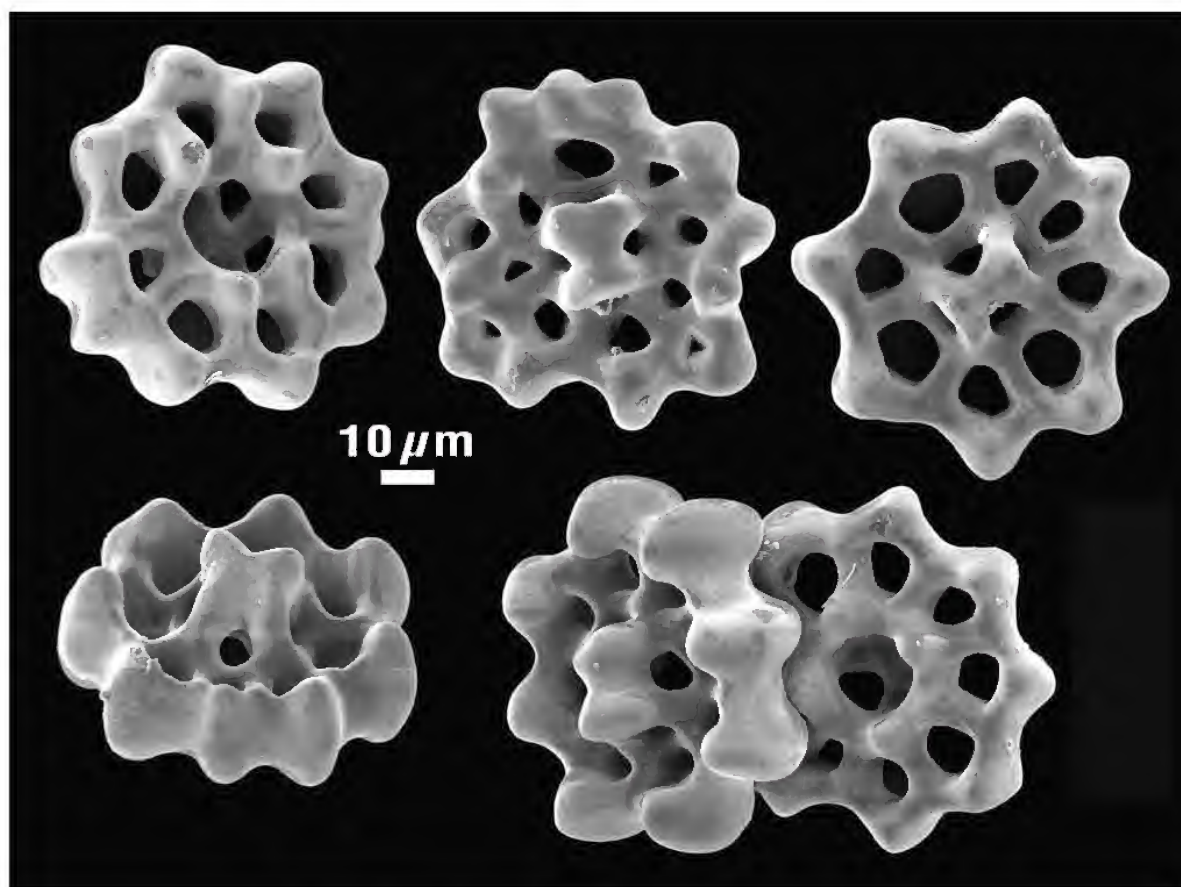


Figure 20. SEM images of ossicles from the mid-body wall of a 35 mm long specimen of a species of *Paracaudina* Heding 1932 from the Chatham Rise (NIWA 70957).

Paracaudina species (not described)

Figure 20

Material examined. East of New Zealand, Chatham Rise, 43.00°S 179.00°W, 546 m, 12 Sep 1989, NIWA 70957 (1); outer east Cook Strait, 41.70°S 175.65°E, 1040–1080 m, 15 Apr 2010, NIWA 63034 (1); 41.51°S 175.72°E, 1076–1104 m, 17 Apr 2010, NIWA 63195 (1); 41.95°S 174.62°E, 964–1005 m, 23 Apr 2010, NIWA 63806 (5).

Remarks. Our colleagues in NIWA (Wellington) inform us of many *Paracaudina* specimens in their collections. We have had the opportunity to examine only eight. Mid-body ossicles from one small specimen (35 mm long; NIWA 70957) are illustrated here. They are not those of *Paracaudina coriacea* (Hutton, 1972) or *Paracaudina chilensis* (Müller, 1850). Nor do the ossicles in the eight specimens appear to be the ossicles of only one species, those from the Chatham Rise specimen differing from those from the outer east Cook Strait specimens. A comprehensive examination of the NIWA *Paracaudina* specimens will be undertaken after this work, presumably in Wellington.

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References

- Bell, F. J. 1883. Studies in the Holothuroidea. II. Descriptions of new species. *Proceedings of the Zoological Society of London*. pp. 58–62, pl. 15.
- Benham, W. B. 1909. Scientific results of the New Zealand Government Trawling Expedition, 1907. Echinoderma. *Records of the Canterbury Museum* 1(2): 83–116, pls 7–11.
- Cannon, L. R. G. and Silver, H. 1986. *Sea Cucumbers of Northern Australia*. viii + 60 pp. Brisbane: Queensland Museum.
- Clark, A. M. and Rowe, F. W. E. 1971. *Monograph of shallow-water Indo-West Pacific echinoderms*. Pp. vii+238, 100 figs, 31 pls. British Museum (Natural History): London.
- Clark, H. L. 1908. The apodous holothurians. *Smithsonian Contributions to Knowledge* 35: 1–231, pls 1–13.
- Clark, H. L. 1914. The echinoderms of the W.A. Museum. *Records of the Western Australian Museum and Art Gallery* 1(3): 132–173, fig. 1, pls 17–26.
- Clark, H. L. 1935. The holothurian genus *Caudina*. *The Annals and Magazine of Natural History* 10(15)86(22): 267–284.
- Clark, H. L. 1938. Echinoderms from Australia. An account of collections made in 1929 and 1932. *Memoir of the Museum of Comparative Zoology, Harvard University* 55: 1–596.
- Clark, H. L. 1946. The Echinoderm Fauna of Australia: Its composition and origin. *Publications Carnegie Institute* 566. 567 pp.
- Deichmann, E. 1938. Holothurians from the Western Coasts of Lower California and Central America, and from the Galápagos Islands. *Zoologica. Eastern Pacific Expeditions of the New York Zoological Society* 23(18): 361–387, figs 1–15.
- Dendy, A. 1897. Observations on the holothurians of New Zealand; with descriptions of four new species, and an appendix on the development of the wheels in *Chiridota*. *Journal of the Linnean Society (Zoology)* 26: 22–52, pls 3–7.
- Dendy, A. 1898. On some points in the anatomy of *Caudina coriacea* Hutton. *Journal of the Linnean Society (Zoology)* 26: 456–464, pl. 29.
- Dendy, A. and Hindle, E. 1907. Some additions to our knowledge of the New Zealand holothurians. *Journal of the Linnean Society (Zoology)* 30: 95–125, pls 11–14.
- Djakonov, A. M., Baranova, Z. I. and Savel'eva, T. S. 1958. Note on the holothurians from south of Sakhalin and the Kuril Islands. *Investigations of the Far Eastern Seas of the U.S.S.R.* 5: 358–380. (In Russian)
- Farquhar, H. 1898. On the echinoderm fauna of New Zealand. *Proceedings of the Linnean Society of New South Wales* 23(91): 300–327.
- Gowlett-Holmes, K. 2008. *A field guide to the marine invertebrates of South Australia*. 333 pp. Tasmania, Hobart, notomares.
- Haeckel, E. H. 1896. *Systematische Phylogenie der Wirbellosen Thiere (Invertebrata)*. Zweiter Theil des Entwurfs einer systematischen Stammesgeschichte. Berlin. 720 pp.
- Heding, S. G. 1931. On the Classification of the Molpadids. Preliminary notice. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 92: 275–284.
- Heding, S. G. 1932. *Paracaudina* nom. nov. a correction, together with some remarks concerning the supposed fossil Holothurian *Pseudocaudina brachyura* Broili. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 92: 455–456.
- Heding, S. G. 1933. The *Caudina* of Asamushi, the so-called *Caudina chilensis* (Johs. Müller). *The Science Reports of Tohoku University* 8(2): 127–142, pls 5–8.
- Hickman, V. V. 1962. Tasmanian sea-cucumbers (Holothuroidea). *Papers and Proceedings of the Royal Society of Tasmania* 96: 49–72, 2 pls, 186 figs.
- Hickman, V. V. 1978. Notes on three species of Tasmanian sea cucumbers including one species that broods its young in the coelome. (Holothuroidea: Phyllophoridae, Caudinidae). *Papers and Proceedings of the Royal Society of Tasmania* 112: 29–37, figs 1–44, 2 pls.
- Hozawa, S. 1928. On the changes occurring with advancing age in the calcareous deposits of *Caudina chilensis* (J. Müller). *The Science Reports of Tohoku University 4 Biology* 3(3)2: 361–378, pls 14–16.
- Hutton, F. W. 1872. *Catalogue of the Echinodermata of New Zealand, with Diagnoses of the Species*. 20 pp. Wellington: James Hughes.
- Hutton, F. W. 1879. Notes on some New Zealand Echinodermata, with descriptions of new species. *Transactions and Proceedings of the New Zealand Institute* 11(31): 305–308.
- Joshua, E. C. 1914. Victorian Holothuroidea, with descriptions of new species. *Proceedings of the Royal Society of Victoria* 27(1): 1–11, 1 pl.
- Joshua E. C. and Creed, E. 1915. South Australian Holothuroidea, with descriptions of new species. *Transactions and Proceedings of the Royal Society of South Australia* 39: 16–24, pls 2–4.
- Lampert, K. 1885. Die Seewalzen. Holothuroidea. Eine Systematische Monographie. In Semper, C. (ed.) *Reisen im Archipel der Philippinen* 4(3): 1–310, 1 pl.
- Lane, D. J. W., Marsh L. M., VandenSpiegel, D., Rowe, F. W. E. 2000. Echinoderm fauna of the South China Sea: an inventory and analysis of distribution patterns. *The Raffles Bulletin of Zoology Supplement* 8: 459–493.
- Liao, Y. and Clark, A. M. 1995. *The echinoderms of southern China*. 614 pp., 23 pls. Science Press: Beijing.
- Ludwig, H. 1883. Verzeichnis der Holothurien des Kieler Museums. *Bericht der Oberhessischen Gesellschaft für Natur- und Heilkunde* 22(6): 155–176.
- Ludwig, H. 1891. Echinodermen. I. Buch. Die Seewalzen. In Dr. H. G. Bronn's *Klassen und Ordnungen des Thier-Reichs* 2(3). 460 pp., 17 pls. Leipzig.
- Ludwig, H. 1898. Holothurien. *Ergebnisse der Hamburger Magalhaensischen Sammelreise 1892/93* 1: 1–98, pls 1–3.
- Mah C. L., McKnight, D. G., Eagle, M. K., Pawson, D. L., Améziane, N., Vance, D. J., Baker, A. N., Clark, H. E. S., and Davey, N. 2009. Phylum Echinodermata. Sea-stars, brittle stars, sea urchins, sea cucumbers, sea lilies. In D. Gordon (Ed.) *New Zealand Inventory of Biodiversity (Volume 1)*. Canterbury University Press, New Zealand.
- Marenzeller von, E. 1881. Neue holothurien von Japan und China. *Verhandlungen Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft, Wien* 31: 121–140 pls 4, 5.
- Mitsukuri, K. 1912. Studies on actinopodous Holothuroidea. *Journal of the College of Science, Tokyo Imperial University* 29(2): 1–284, 8 pls.
- Mortensen, Th. 1925. Echinoderms of New Zealand and the Auckland-Campbell Islands. III–V. Asteroidea, Holothuroidea, Crinoidea. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København* 79(29): 261–420, text figs 1–70, pls 12–14.

- Müller, J. 1850. Anatomische Studien über die Echinodermen. *Archiv für Anatomie, Physiologie und wissenschaftliche Medizin* 1850: 117–155.
- Müller, J. 1854. Über den Bau der Echinodermen. *Abhandlungen Berliner Königlich Preussischen Akademie* 1853. 40 pp, 9 pls. Berlin.
- Ohshima, H. 1929. The Caudina of Asamushi. *Contributions from the Zoological Laboratory, Kyushu Imperial University* 18: 39–45.
- Pawson, D. L. 1963. The holothurian fauna of Cook Strait, New Zealand. *Zoology Publications from Victoria University of Wellington* 36: 1–38, 7 figs.
- Pawson, D. L. 1965. The bathyal holothurians of the New Zealand region. *Zoology Publications from Victoria University of Wellington* 39: 1–33, 7 figs.
- Pawson, D. L. 1969. Holothuroidea from Chile. Report No. 46 of the Lund University Chile Expedition 1948–1949. *Sarsia* 38: 121–145.
- Pawson, D. L. 1970. The marine fauna of New Zealand: Sea cucumbers (Echinodermata: Holothuroidea). *Bulletin of the New Zealand Department of Scientific and Industrial Research* 201: 7–65, 10 figs, 2 pls.
- Pawson, D. L. 1977. Molpadiid sea cucumbers (Echinodermata: Holothuroidea) of the southern Atlantic, Pacific and Indian Oceans. *Biology of the Antarctic Seas VI. Antarctic Research Series* 26: 97–123.
- Pawson, D. L. and Liao, Y. 1992. Molpadiid sea cucumbers of China, with descriptions of five new species (Echinodermata: Holothuroidea). *Proceedings of the Biological Society of Washington* 105(2): 373–388.
- Pawson, D. L., Vance, D. J. and Ahearn, C. 2001. Western Atlantic sea cucumbers of the Order Molpadiida (Echinodermata: Holothuroidea). *Bulletin of the Biological Society of Washington* 10: 311–327.
- Perrier, R. 1904. Holothuries du Cap Horn. *Bulletin du Muséum d'Histoire Naturelle, Paris* 10: 13–17.
- Perrier, R. 1905. Holothuries antarctiques du Muséum d'Histoire naturelle de Paris. *Annales Sciences Naturelles, Zoologie* 9(1): 146 pp., 5 pls.
- Rowe, F. W. E. 1982. Sea-cucumbers (class Holothuroidea). In Shepherd, S. A. and Thomas, I. M. (eds), *Marine Invertebrates of Southern Australia* 1: 454–476, figs 10: 26–10:37, pls 29–32. Adelaide, South Australian Government Printer.
- Rowe, F. W. E. and Gates, J. 1995. Echinodermata. In Wells, A. (ed.), *Zoological Catalogue of Australia* 33: i–xiii, 1–510. CSIRO, Melbourne.
- Saunders, B. 2009. *Shores and Shallows of Coffin Bay. An Identification Guide. Government of South Australia. Eyre Peninsula Natural Resources Management Board.* 152 pp. Australian Printing Specialists, South Australia.
- Semper, C. 1868. Holothurien. *Reisen im Archipel der Philippinen* 1: 1–288, pls 1–40.
- Sluiter, C. 1880. Ueber einige neue Holothurien von der West-küste Java's. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 40: 333–358, pls 1–7.
- Théel, H. 1886. Report on the Holothuroidea dredged by H. M. S. *Challenger* during the years 1873–1876. *Report on the scientific results of the voyage of H. M. S. Challenger, Zoology* 14(39): 1–290, 16 pls.

What is *Alloxysta fulviceps* (Curtis, 1838) (Hymenoptera: Cynipoidea: Figitidae: Charipinae)?

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Abstract

Pujade-Villar, J., Ferrer-Suay, M., Selfa, J. and Alonso-Zarazaga, M.A. 2011. What is *Alloxysta fulviceps* (Curtis, 1838) (Hymenoptera: Cynipoidea: Figitidae: Charipinae)? *Memoirs of Museum Victoria* 68: 67–70.

The validity of *Alloxysta fulviceps* (Curtis, 1838) and its synonymies have been examined. After studying the type series and the taxonomic history of this species, we conclude that the lectotype was wrongly designated. A new lectotype is designated and *A. fulviceps* is synonymised with *A. victrix* (Westwood, 1833).

Keywords

Hymenoptera, Figitidae, Charipinae, *Alloxysta fulviceps*

Introduction

The Charipinae (Hym., Figitidae) species *Alloxysta fulviceps* (Curtis, 1838) has been a troublesome species since its description. Curtis (1838, p. 688) described it as a species of *Cynips* with the following features: ‘27. *fulviceps* Curt. Shining black, head and legs bright ochre; antennae longer than the body, fuscous, base ochreous, 2 basal joints ovate, 3rd slender, scarcely longer than the following, wings very ample: 2/3 long. Bred from female Aphides by the late Mr. T. Carpenter’.

Later, it was transferred to *Allotria* by Kieffer (1900, p. 114). According to Kieffer (1902, p. 76), this species was considered as doubtful and insufficiently described. It was kept in *Allotria* by Dalla Torre and Kieffer (1902, p. 41), and finally it was transferred by Dalla Torre and Kieffer (1910, p. 288) to *Charips*.

Quinlan and Fergusson (1981) mentioned that the type series deposited in Museum Victoria (Australia) was studied by Kerrich in 1948. According to these authors, this type series consisted of three specimens, and Kerrich defined one of them as ‘type of *Cynips fulviceps* = *Alloxysta fulviceps*’. These data were not published and Fitton (1978, p. 65) was the first to consider Curtis’s species in *Alloxysta*.

According to Quinlan and Fergusson (1981), the type series of *A. fulviceps* grouped two distinct morphologies: 1 ♀ with Kerrich’s notes (with open radial cell) and 2 ♀ without Kerrich’s notes (with closed radial cell). These two specimens were labelled by Quinlan with the following notes: ‘*Alloxysta*

minuta? (Hrt.) ♀ det. Quinlan 1986’ and ‘this specimen has not type-status’. Since then, Curtis’s species has been a species with an open radial cell (a feature not mentioned by Curtis in his description).

In the same study, Quinlan and Fergusson (1981) synonymised *Alloxysta erythrothorax* (Hartig, 1840) with *A. fulviceps*. This synonymy has two problems: (1) the choice as lectotype of the specimen with an open radial cell, when Curtis did not mention the morphology of the radial cell, and (2) the distinct chromatic features that are mentioned in the original description of *Alloxysta fulviceps* (Curtis) and *A. erythrothorax* (Hartig). Hartig (1840, p. 200) defined *Xystus erythrothorax* as follows: ‘5) *X. erythrothorax* m.: niger, capite rufo; facie flava, pectore rufo; antennis pedibusque rufis. Male’.

Results and discussion

None of the aforementioned authors did a redescription of Curtis’s species, so we borrowed the type material from Museum Victoria. Only one of the three original specimens remains (Catriona McPhee, Collection Manager Terrestrial Invertebrates (Mon-Wed) of the Museum Victoria, pers. com. on 21 Feb. 2011): one of the two of the original series (before Kerrich’s study) that has a closed radial cell. We are not able to determine how Kerrich chose a lectotype of *Cynips fulviceps*, but after Quinlan’s study and the synonymy proposed by Quinlan and Fergusson (1981), this specimen would have to have a reddish yellow mesoscutum. Therefore, it cannot be the lectotype of *A. fulviceps* because Curtis



Figure 1. Lateral view of the designated lectotype of *Alloxysta fulviceps* (Curtis).

stated that the mesoscutum is completely black. For these reasons, we must consider that the specimen that was chosen as lectotype does not fit the original description by Curtis. On the other hand, we have examined the one remaining specimen of Curtis's type series, which corresponds exactly with Curtis's description. In summary, we designate here a new lectotype for *Alloxysta fulviceps* (= *Cynips fulviceps* Curtis), which has the following labels: '*Alloxysta minuta*? (Hrt.) ♀ det. Quinlan 1986' (white label), 'this specimen has not type-status' (white label), 'MUS. VIC. ENTO 2011-4-L' (green label), 'this specimen has type status JP-V, 2011', '27 *Cynips fulviceps* bred from Aphides female by Aphidius? T.C. 13 July 26 — [unreadable] Dorset. Bred from aphids of Willows and Cow Parsnip Hal' (photocopy of Curtis original annotations of his notebook), 'lectotype of *Cynips fulviceps* Curtis, 1838 ♀, designed J.P-V 2011' (red label), '*Alloxysta victrix* (Westwood, 1833) Ferrer-Suay det-2011 (white label).

Our study of this material also shows that *A. fulviceps* is the same species as *A. victrix*. Therefore, in this study, the synonymy of *A. fulviceps* and *A. erythrothorax* is removed, a

new lectotype for *A. fulviceps* is established, this species is synonymised with *A. victrix* and the validity of *A. erythrothorax* (Hartig) is re-established.

The taxonomic changes we propose restructure the list of synonyms and valid species implied, so we present it here:

Alloxysta erythrothorax (Hartig, 1840) Dalla Torre and Kieffer, 1902

Xystus erythrothorax (Hartig, 1840, p. 200). Synonymised by Quinlan and Fergusson (1981, p. 254). Type: ZSBS (according to Evenhuis, 1982, p. 23).

Xystus defectus (Hartig, 1841, p. 352). Synonymised by Fergusson (1986, p. 10). Type: ZSBS (according to Evenhuis, 1982, p. 22).

Allotria nigriventris (Thomson, 1862, p. 409). Synonymised by Fergusson (1986, p. 10). Type: MZLU (according to Andrews, 1978, p. 87).

Comments: Hellén (1963) redescribed *A. erythrothorax* and *A. defecta*. The latter was synonymised with the former by Fergusson (1986). The two species match chromatically. Fergusson (1986) also synonymised *A. nigriventris* (Thomson)

with *A. erythrothorax*, and according to Kieffer (1902), the mesosoma of *A. nigriventris* is reddish; this also matches *A. erythrothorax*.

Alloxysta victrix (Westwood, 1833) Hellén, 1963

Allotria victrix (Westwood, 1833, p. 495). Type: OXUM (according to Andrews, 1978, p. 92).

Cynips fulviceps (Curtis, 1838, p. 688). Type: NMVM **n. syn.**

Cynips ruficeps (Zetterstedt, 1838, p. 410). Synonymised by Giraud (1860, p. 127). Type: MZLU (according to Evenhuis and Kiriak, 1985, p. 16).

Xystus erythrocephalus (Hartig, 1840, p. 199). Synonymised by Giraud (1860, p. 127). Type: ZSBS (according to Evenhuis, 1972, p. 211).

Allotria tritici (Fitch, 1861, p. 841). Synonymised by Menke and Evenhuis (1991, p. 147). Type: USNM (according to Menke and Evenhuis, 1991, p. 147).

Allotria (Allotria) macrocera (Thomson, 1877, p. 814). Synonymised by Dalla Torre and Kieffer (1910, p. 285). Type: MZLU (according to Hellén, 1963, p. 4).

Allotria curvicornis (Cameron, 1883, p. 366). Synonymised by Fergusson (1986, p. 11). Type: BMNH (according to Quinlan, 1978, p. 124).

Allotria (Allotria) luteicornis (Kieffer, 1902, p. 15). Synonymised by Evenhuis and Barbotin (1987, p. 217). Type: NHM, Amiens (according to Dessart, 1969, p. 193).

Allotria (Allotria) victrix var *luteiceps* (Kieffer, 1902, p. 16). Synonymised by Evenhuis and Barbotin (1987, p. 217). Type: NHM, Amiens (according to Dessart, 1969, p. 194).

Allotria (Allotria) luteicornis var *lateralis* (Kieffer, 1902, p. 70). Synonymised by Evenhuis and Barbotin (1987, p. 216). Type: NHM, Amiens (according to Dessart, 1969, p. 193).

Charips areolata (Kieffer, 1909, p. 481). Synonymised by Menke and Evenhuis (1991, p. 145). Type: USNM (according to Menke and Evenhuis, 1991, p. 145).

Sarothrus io (Girault, 1932, p. 3). Synonymised by Paretas-Martínez and Pujade-Villar (2010, p. 355). Type: QM (according to Paretas-Martínez and Pujade-Villar, 2010, p. 355).

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References

Andrews, F. G. 1978. Taxonomy and host specificity of Nearctic Alloxystinae with a catalogue of the World species (Hymenoptera: Cynipidae). *Occasional Papers in Entomology* 25: 1–128.

Cameron, P. 1883. Descriptions of sixteen new species of parasitic Cynipidae, chiefly from Scotland. *Transactions of the Entomological Society of London* 16(4): 365–374.

Curtis, J. 1838. *British entomology: being illustrations and descriptions of the genera of insects found in Great Britain and Ireland: containing coloured figures from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found*, vol. 1. Privately published, London. 15: 674–721.

Dalla Torre, K. W. and Kieffer, J. J. 1902. Cynipidae. Pp. 1–84 in: Wytsman, P. *Genera Insectorum, Vol. I*. Brussels.

Dalla Torre, K. W. and Kieffer, J. J. 1910. *Das Tierreich XXIV: Cynipidae*. R. Friedlander and Sons: Berlin. 24: 891 pp.

Dessart, P. 1969. Les types de Cynipidae décrits par l'abbé Jean-Jaques KIEFFER, conservés dans la collection Léon CARPENTIER au Musée d'Histoire naturelle d'Amiens (France). *Bulletin et Annales de la Société Royale Entomologique de Belgique* 105.

Evenhuis, H. H. 1972. Studies on Cynipidae Alloxystinae. 2. The identity of some species associated with aphids of economic importance. *Entomologische Berichten* 32: 210–217.

Evenhuis, H. H. 1982. A study of Hartig's *Xystus* species with type designations and new synonyms (Hymenoptera: Cynipidae Alloxystinae and Charipinae). *Spixiana* 5: 19–29.

Evenhuis, H. H. and Barbotin, F. 1987. Types des espèces d'Alloxystidae (Hymenoptera, Cynipoidea) de la collection Carpentier, décrits par J. J. Kieffer, avec synonymes nouveaux et un nomen novum. *Bulletin et Annales de la Société Royale Belge* 123: 211–224.

Evenhuis, H. H. and Kiriak, I. G. 1985. Studies on Alloxystidae (Hymenoptera, Cynipoidea) 8. *Cynips minuta* Zetterstedt and *Xystus minutus* Hartig. *Entomologische Berichten* 45: 16–20.

Fergusson, N. D. M. 1986. Charipidae, Ibaliidae and Figitidae (Hymenoptera: Cynipoidea). *Handbook of Identification British Insects* 8(1c): 1–55.

Fitch, A. 1861. Sixth report on the noxious and other insects of the state of New York. *Transactions of New York State, Agricultural Society* 20: 745–868.

Fitton, M. G. 1978. A check list of British insects by George Sidney Kloet and the late Walter Douglas Hincks, 2nd edition (completely revised). Part 4: Hymenoptera. *Handbooks for the Identification of British Insects* 11(4): 159 pp.

Giraud, J. 1860. Enumeration des Figitides de l'Autriche. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* 10: 123–176.

Girault, A. A. 1932. *New lower Hymenoptera from Australia and India*. Private publication, Brisbane. 6 pp.

Hartig, T. 1840. Ueber die Familie der Gallwespen. *Zeitschrift für Entomologie* (Germar) 2: 176–210.

Hartig, T. 1841. Erster nachtrag zur naturgeschichte der Gallwespen. *Zeitschrift für Entomologie* (Germar) 3: 322–358.

Hellén, W. 1963. Die Alloxystininen Finnlands (Hymenoptera: Cynipidae). *Fauna Fennica* 15: 1–23.

Kieffer, J. J. 1900. Ueber Allotrinen. *Wiener Entomologische Zeitung* 19: 112–115.

Kieffer, J. J. 1902. Les Cynipides (part 2). Pp. 5–78 in: Andre, E (ed.), *Species des Hyménoptères d'Europe et d'Algérie* 7(2). 748 pp, 21 pl.

Kieffer, J. J. 1909. Beschreibung neuer in Blattläusen schmarotzender Cynipiden. *Naturwissenschaftliche Zeitschrift für Forsten und Landwirtschaft Stuttgart* 7: 479–482.

Menke, A. S. and Evenhuis, H. H. 1991. North American Charipidae: key to genera, nomenclature, species checklists, and a new species of *Dilyta* Förster (Hymenoptera: Cynipoidea). *Proceedings of the Entomological Society of Washington* 93: 136–158.

Paretas-Martínez, J. and Pujade-Villar, J. 2010. First valid records of Figitinae (Hymenoptera: Figitidae) from Australia: *Xyalophora mauri* sp. n. and *Xyalophora australiana* sp. n. *Australian Journal of Entomology* 49: 354–358.

Quinlan, J. 1978. On the identity of some British Alloxystinae described by P. Cameron and by J. J. Kieffer (Hymenoptera, Cynipidae). *Entomologische berichten* 38: 71–74.

- Quinlan, J. and Fergusson, N. D. M. 1981. The status and identity of the Cynipoidea (Hymenoptera) described by J. Curtis. *Entomological Gazette* 32: 251–256.
- Thomson, C. G. 1862. Forsök till uppställning och beskrifning af Sveriges Figiter. *Öfversigt af Kongl. Svenska Vetenskaps-Akad: s förhandl* 18: 395–420.
- Thomson, C. G. 1877. Ofversikt af Sveriges Cynips-arter. *Opuscula Entomologica* 8: 778–820.
- Westwood, J. O. 1833. Notice of the habits of a Cynipidous insect parasitic upon the *Aphis rosae* with descriptions of several other parasitic Hymenoptera. *Magazine of Natural History* 6: 491–497.
- Zetterstedt, J. W. 1838. *Insecta Lapponica descripta: Hymenoptera*. Voss, Lipsiae. 315–476 pp.

Review of the genus *Monotheca* (Hydrozoa: Leptolida) from Australia with description of a new species and a note on *Monothecella* Stechow, 1923

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Abstract

Watson, J.E. 2011. Review of the genus *Monotheca* (Hydrozoa: Leptolida) from Australia with description of a new species and a note on *Monothecella* Stechow, 1923. *Memoirs of Museum Victoria* 68: 71–91.

Monotheca Nutting, 1900 is a genus with few known species worldwide. It is an artificial genus, as some species of the Plumulariidae sometimes have one or two hydrocladial hydrothecae and are thus borderline between *Monotheca* and *Plumularia*. This review considers only Australian species with consistently monothecate hydrocladia; species with more than one hydrotheca on the hydrocladium are considered to belong to *Plumularia*. Ten species referable to *Monotheca* are reported from southeast Australia; three are synonymised here in other species, four are presently known to be endemic to Australia and one species, *Monotheca amphibola*, is described as new. The gonosome of *Monotheca togata* is described for the first time. *Monothecella* is synonymised in *Monotheca*. A key to the Australian species of *Monotheca* is given.

Keywords

Monotheca, artificial genus, eight Australian species, key to species; *Monothecella* synonymised.

Introduction

Monotheca Nutting, 1900 (type species *Monotheca margaretta* Nutting, 1900) is an artificial genus; Vervoort and Watson (2003) list 10 species and Bouillon et al. (2006) list eight species worldwide. Other authors, such as Millard (1975) and Hirohito (1995), synonymised *Monotheca* in *Plumularia*. In their phylogeny, Leclère et al. (2007) demonstrated that *Monotheca* with monohydrothecate hydrocladia (*M. pulchella*, *M. margaretta*, *M. obliqua*) form a distinct clade within the Plumulariidae.

Species of *Monotheca* reported from Australia are *Monotheca obliqua* (Johnston, 1847), *Monotheca australis* (Kirchenpauer, 1876), *Monotheca compressa* (Bale, 1882), *Monotheca hyalina* (Bale, 1882), *Monotheca pulchella* (Bale, 1882), *Monotheca spinulosa* (Bale, 1882), *Monotheca aurita* (Bale, 1888), *Monotheca flexuosa* (Bale, 1894), *Monotheca obesa* (Blackburn, 1938) and *Monotheca togata* (Watson, 1973). Four of these species — *M. hyalina*, *M. pulchella*, *M. spinulosa* and *M. togata* — are also reported from New Zealand (Vervoort and Watson 2003). A new species, *Monotheca amphibola* sp. nov., from seagrass habitat in southeast Australia, is described here. Some species assigned to *Monotheca* — for example, *Plumularia excavata* (Mulder and Trebilcock, 1910), *Plumularia crateriformis* (Mulder and Trebilcock, 1910), *Plumularia epibracteolosa* Watson, 1973 and *Plumularia meretricia* Watson, 1973 sometimes have two hydrothecae on the hydrocladium and are thus borderline between *Monotheca* and *Plumularia* as defined here. In this

review, only strictly monohydrothecate species are considered, and species that sometimes have more than one hydrotheca on the hydrocladium are referred to *Plumularia*.

Although several species of *Monotheca* from Australia discussed in this paper as presently known are endemic to Australia there are some exceptions. These include *M. obliqua* known from the *Posidonia oceanica* seagrass meadows of the Mediterranean Sea (Boero 1981a, Boero et al. 1985; Fresi et al. 1982, Bouillon et al. 2004), the eastern Atlantic (Calder 1997) and Japan (Hirohito 1983); *M. spinulosa* is known from South Africa, the South Atlantic (Millard 1975) and Japan (Yamada 1959, Hirohito 1995); and *M. flexuosa* (as *M. pulchella*, see later discussion) is reported from the Mediterranean Sea and South Africa (Millard 1975). A key to species of *Monotheca* is given.

With the exception of *Monotheca flexuosa*, which is an opportunistic species occurring on many substrates, all Australian species of *Monotheca* are epiphytic — *M. obliqua*, *M. spinulosa* and *M. hyalina* are associated with algae, while *M. australis*, *M. compressa*, *M. obesa* and *M. amphibola* sp. nov. occur on seagrasses. New Zealand species recorded as *M. hyalina* and *M. flexuosa* (see later discussion concerning their identity) are from algae.

Monothecella Stechow, 1923.

Stechow (1923a) erected the genus *Monothecella* for three species (*Monotheca australis* Kirchenpauer, 1876; *Monotheca aurita* Bale, 1888; *Monotheca compressa* Bale, 1882), all of

which have a hydrocladial median inferior nematotheca on a stout immovable base. The term monothalamic is usually applied to this structure, assuming that the distal cup is openly contiguous with its supporting peduncle. Detailed examination of fresh, preserved and mounted material of this suite of species (synonymised in *M. australis*, see discussion later) clearly shows that the cup is seldom completely open, and there is usually a faint line of demarcation between the cup and its base. The term monothalamic is therefore abandoned in the present context and the nematothecae regarded as incipiently bithalamic. For this reason, the genus *Monotheccella* is untenable and is here synonymised in *Monothecca*.

Material.

In the following account, a large amount of material collected over four decades by the author and others around Australia is examined. Material is held in the collections of Museum Victoria, Melbourne, Australia (NMV), the Australian Museum, Sydney (AM), the South Australian Museum (SAM), the Western Australian Museum (WAM), the National Museum of New Zealand (NMNZ) and in the author's personal collection.

Family Plumulariidae McCrady, 1859

Monothecca Nutting, 1900

Colony small, caulus erect, monosiphonic, simple or sparingly branched, divided into internodes without hydrothecae. Hydrocladia alternate, consisting of two internodes, the distal one bearing a hydrotheca with one median inferior nematotheca and two superior lateral nematothecae seated on a distal enlargement or a bifurcation of the internode. Gonangia fixed sporosacs, usually borne on proximal part of the stem, ovate or sac shaped, without protective appendages.

Monothecca amphibola sp. nov.

Fig. 1A–G

Material examined. NMV F147479, holotype, microslide (malinol mounted), fertile colony from leaves of the seagrass *Amphibolis antarctica*, 200 m offshore from Queenscliff, Victoria, depth 2 m, coll: J. Watson 23 March 2008. NMV F147481, remainder of holotype colony, alcohol preserved. Paratype, NMV F147480, microslide (malinol mounted), fertile colony on leaves of the seagrass *Amphibolis antarctica*, 200 m offshore from Queenscliff, Victoria, depth 2 m, coll: J. Watson 23 March 2008.

Description from holotype and paratype. Stems to 3.5 mm long, monosiphonic, arising at regular intervals from hydrorhiza running more or less straight up seagrass leaf; stolons wide, ribbon-like with a narrow perisarcal flange with numerous internal flexion joints. Proximal stem with four or five strong transverse joints, succeeding cauline internodes variable in length, longer on taller stems, perisarc smooth and thick with several strong, more or less equally spaced transverse internal septa, nodes broad V-shaped overlapping joints.

Hydrocladia alternate, distal on cauline internode, on a short, strong apophysis, directed almost perpendicularly

outward from stem, distal node of apophysis slightly oblique to transverse; proximal hydrocladial internode short, athecate, distal node strongly oblique.

Hydrothecate internode moderately long and deep with two distinct internal opposing septa; hydrotheca distal on internode, facing upward at an angle of c. 45° to hydrocladium; cup shaped, slightly broader than deep, adcauline wall weakly concave to straight, abcauline wall distinctly concave, margin circular, entire, rim not everted, perisarc thin, a large sinuous abcauline perisarc flange passing from margin downwards to beyond base of hydrotheca; a smaller triangular adcauline flange passing from hydrothecal margin to hydrocladium.

Nematothecae small, bithalamic, one on cauline internode, about one-third distance up internode and on same side as hydrocladium, base moderately long, adpressed to internode, cup slightly adcaudally excavated, one axillar, on front of stem beside apophysis, cup slightly elliptical, one hydrocladial median inferior on hydrothecate internode, not moveable, base long, stout and bent, cup small, adcaudally excavated and adpressed to flange of internode, not quite reaching base of hydrotheca; twin laterals standing erect, distal on hydrocladium below hydrothecal flange but not reaching hydrothecal margin, cups slightly adcaudally shortened; stolonial nematothecae scattered along hydrorhiza, base long, slightly tapering, cup circular, shallow.

Male and female gonothecae often borne on opposite sides of same caulus, large, similar in shape, irregularly ovoid, borne on a pedicel inserted below proximal stem apophysis; some gonothecae recumbent to substrate, others standing out perpendicular to stem; walls of gonotheca smooth, no distinct operculum, a thin diagonal apical fold usually marking site of future rupture; female gonophore packed with many moderately large ova.

Monothecca amphibola, measurements (µm)

Hydrorhiza, width	160–170
Stem internode	
length	272–360
width at node	36–40
Apophysis, adcauline length	32–56
diameter at distal node	40–52
Hydrocladium	
length adcauline athecate segment	32–36
basal length of thecate internode	176–200
Hydrotheca	
length, base to margin along axis	100–108
diameter at margin	116–128
Nematotheca	
cauline, length of base	40–50
cauline, depth of cup	28–20
cauline, diameter of cup	28–32
axillar, length of base	30–36
axillar, depth of cup	12–14
axillar, diameter of cup	28–34

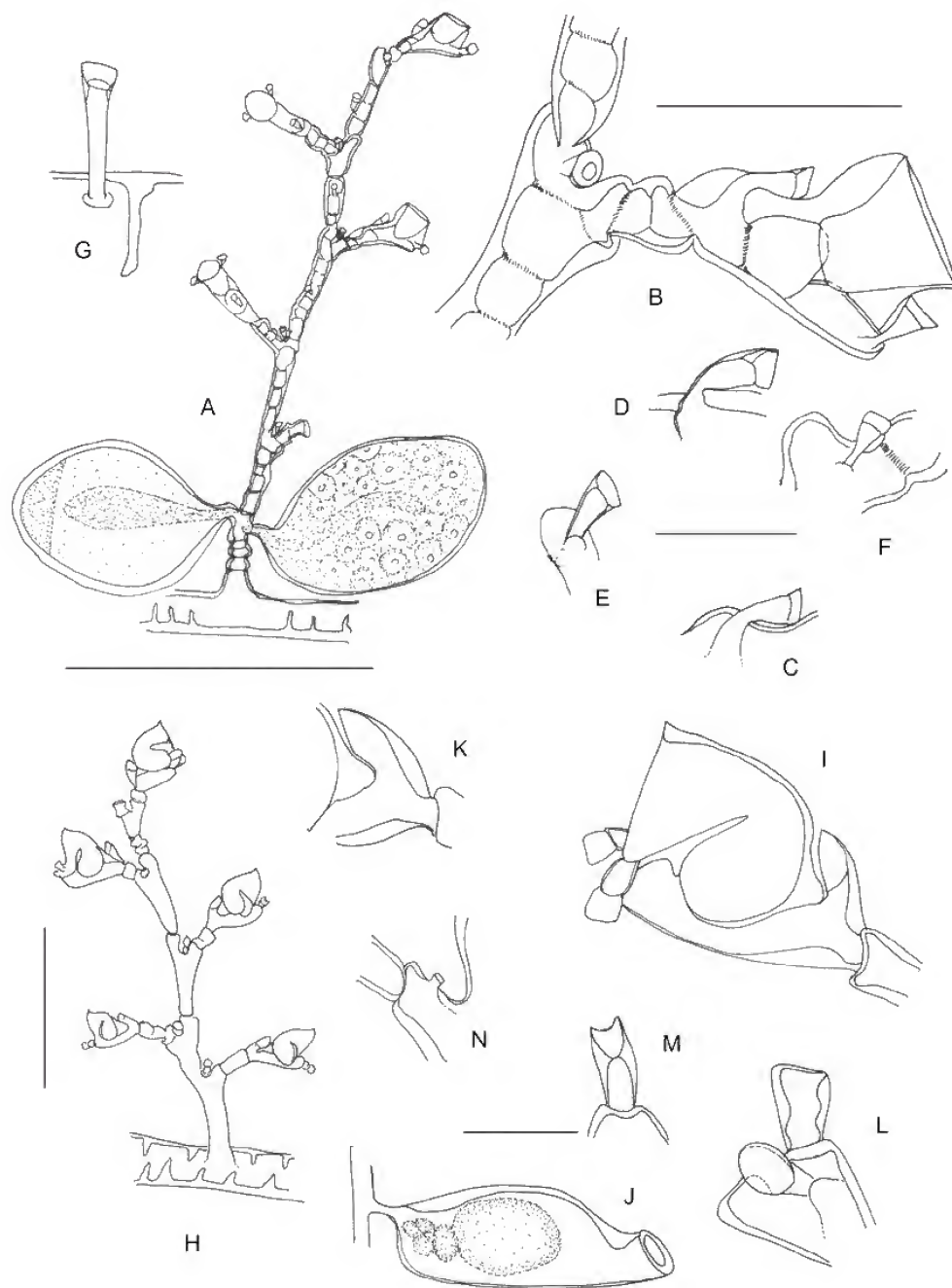


Figure 1. A–G, *Monothecha amphibola* sp. nov. (drawn from holotype and paratypes). A, fertile stem with male and female gonothecae; B, hydrocladium and hydrotheca; C, median inferior nematotheca; D, cauline nematotheca; E, one of twin lateral nematothecae; F, axillar nematotheca; G, hydrorhizal nematotheca. H–N, *Monothecha australis*. H, infertile stem; I, hydrocladium and hydrotheca; J, female gonotheca with developing larva; K, median inferior nematotheca. Note clear demarcation between cup and peduncle (I) and its absence (K); L, axillar nematotheca; M, one of twin lateral nematothecae; N, axillar hydrostatic pore (axillar nematotheca not shown). Scale bar: A, 1 mm; B, I, H, 0.2 mm; C–G, K–N, 0.1 mm; J, 0.5 mm.

median, length of base	34–40
median, depth of cup	12–16
median, diameter of cup	30–34
lateral, length of base	38–42
lateral, depth of cup	10–16
lateral, diameter of cup	36–40
hydrorhizal, length of base	98–100
hydrorhizal, depth of cup	30–32
hydrorhizal, diameter of cup	28–36

Remarks. The Mulder and Trebilcock collection in Museum Victoria contains five microslides (Canada Balsam-mounted) labelled '*Plumularia setaceoides* var. *crateriformis*, 1910'. Two of these slides are labelled 'type' by Mulder and Trebilcock (see Mulder and Trebilcock 1910, p. 118). The locality of the specimens is Bream Creek on the central Victorian coast. Unfortunately, the specimens are so badly fragmented that it is impossible to determine whether they were originally *Plumularia* or *Monothecha*. These, and a third slide from the same series (NMV F57987, F57988, F57989), were designated syntypes by Stranks (1993). I select the best of these (F57987) as lectotype of *Plumularia setaceoides* var. *crateriformis*.

Stechow (1925) raised the var. *crateriformis* to specific rank, recording the species from brown algae at 12–14 m depth in Warnbro Sound, Western Australia. Watson (2005) also reported *P. crateriformis* from algae at 16 m depth in the nearby Archipelago of the Recherche, Western Australia. *Plumularia nodosa* Stechow, 1924, also from Western Australia, is probably conspecific with *P. crateriformis*; however as neither species is referable to *Monothecha* as defined here, they are not considered any further.

Two of the three remaining Mulder and Trebilcock microslides are labelled '*Plumularia setaceoides* var. *crateriformis*, Bream Creek, January 1914' and are presumably those on which Mulder and Trebilcock (1915) based their augmented description of the var. *crateriformis*. The third slide is labelled '*Plumularia setaceoides* var. *crateriformis*, Torquay, February 1915'. The Bream Creek specimens have only one hydrotheca on the hydrocladium and are referable to *Monothecha*, whereas the Torquay specimen has more than one hydrocladial hydrotheca and thus belongs to *Plumularia*. The 1914 Bream Creek specimens are identical to *Monothecha amphibola* from Queenscliff.

The conspicuous anterior and posterior hydrothecal flanges of *Monothecha amphibola* resemble those in some of the smaller and more variable forms of the *Plumularia setaceoides* species group. These structures, together with the strong internal cauline segmentation and the wide, flat hydrorhiza with flexion joints are adaptations to strengthen the hydrocaulus in the high-energy *Amphibolis* seagrass habitat. The tall hydrorhizal nematothecae are probably for defence against the many grazing predators in the seagrass habitat. The smooth texture of the gonothecal wall is visible only in fresh material, as the gonothecae tend to crumple and become corrugated in mounting.

Etymology. The species is named for the seagrass *Amphibolis antarctica* upon which it grows.

Monothecha australis (Kirchenpauer, 1876)

Fig. 1H–N

Plumularia obliqua var. *australis* Kirchenpauer, 1876: 49, pl. 6, fig. 10.— Von Lendenfeld, 1885a: 474.— Stranks, 1993: 8.

Plumularia australis Bale, 1884: 143, pl. 12, figs 7, 8.— Von Lendenfeld, 1885a: 475.— Bartlett, 1907: 42.— Mulder and Trebilcock, 1916: 77, pl. 10, figs 1–1b.— Bedot, 1921: 26.— Stechow, 1921: 260.— Blackburn, 1938: 316.— Blackburn, 1942: 108.— Watson, 1973: 189.— Staples and Watson, 1987: 218.— Watson, 1992: 220.

Plumularia compressa Bale, 1882: 31, pl. 15, fig. 5.— Bale, 1884: 142, pl. 12, figs 9, 10, pl. 19, figs 39, 40.— Von Lendenfeld, 1885a: 475.— Stranks, 1993: 9.

Plumularia aurita Bale, 1888: 784, pl. 19, figs 16–19.

Monotheccella australis— Stechow, 1923a: 13.— Stechow, 1923b: 221.— Leloup, 1932: 160.

Monothecha australis.— Watson, 2003: 252.

Material examined. The Kirchenpauer dry hydroid collection in Museum Victoria holds material (NMV F58239) labelled (presumably in Kirchenpauer's handwriting) '*Monopyxis australis* Port Phillip (Australien) on *Zostera* sp. c. 1865'.

Material in author's collection: i) from the seagrasses *Amphibolis antarctica* and *Amphibolis griffithi*; Torquay, Victoria, depth 3 m, 7 June 1970. Queenscliff, Victoria, depth 3 m, coll: J. Watson, 15 October 1986. Portland, Victoria, depth 3 m, 14 May 1969. Tipara Reef, Gulf St Vincent, South Australia, depth 5 m, coll: J. Watson, 24 November 1970. Starvation Bay, Western Australia, depth 2 m, coll: J. Watson, 11 January 1986. Point Peron, Western Australia, depth 3 m, coll: J. Watson, 26 January 1986. Whitfords Reef, Marmion, Western Australia, depth 4 m, coll: J. Watson, 6 February 1986. Cockburn Sound, Western Australia, depth 6 m, 12 October 1983. Starvation Bay, Western Australia, depth 6 m, coll: J. Watson, 13 January 1986. ii) from seagrasses *Posidonia australis* and *Posidonia sinuosa*; Gulf St Vincent, South Australia, depth 10 m, coll: J. Watson, 14 December 1968. Gulf St Vincent, South Australia, depth 12 m, 10 November 1968. Whitfords Reef, Marmion, Western Australia, depth 3 m, coll: J. Watson, 22 November 1983. Whitfords Reef, Marmion, Western Australia, depth 24 m, coll: J. Watson, 30 January 1986.

Description (from mounted and preserved material). Stems to 7 mm high, arising from a hydrorhiza reptant on seagrass leaf, stolons broad and flat with flexion joints. Stems monosiphonic, unbranched, sometimes with a short athecate basal internode, following internodes all of same length, cylindrical, smooth, widening to distal apophysis; node above apophysis transverse, narrow.

Hydrocladia alternate, in one plane, one distal on internode, given off below node on an upwardly directed apophysis with slightly oblique distal node. Hydrocladium with a short proximal athecate internode with thick walls and a strong, almost transverse distal node, hydrothecate internode considerably longer than athecate internode, base slightly convex, distal end blunt, ending below hydrothecal margin, no intranodal septa.

Hydrotheca seated in a concavity of internode, occupying almost entire internode, slightly laterally compressed, posterior quarter of abcauline wall strongly convex, then becoming straight to margin, base of hydrotheca divided into two segments by a strong intrathecal septum passing obliquely backwards into hydrotheca from margin, a small circular foramen in floor of hydrotheca, location variable from mid-

base to posterior of hydrotheca; margin perpendicular to or slightly oblique to hydrocladial axis, rim weakly to noticeably sinuous, margin slightly everted with thickened perisarc.

Nematothecae of two different shapes and sizes: one cauline similar to laterals in axil of hydrocladial apophysis, a small cylindrical hydrostatic pore (mamelon of former authors) on apophysis beside base of nematotheca; one hydrocladial median inferior on hydrothecate internode between base of hydrotheca and node, base robust, cup incipiently bithalamic, scoop shaped, sometimes without a line of demarcation between cup and base, closely adpressed to wall of hydrotheca, a distinct flange connecting abcauline wall with internode; twin lateral nematothecae bithalamic, directed outwards or downwards in front of hydrotheca, base large, cup excavated adcaudally to base.

One to three gonothecae borne on lower stem, male and female often on same stem; gonothecae large, turgid, inserted on a short, smooth pedicel below apophysis, standing out perpendicularly from stem or recumbent to substrate, abcauline (upper) wall inflated, adcauline wall straight to weakly convex, body narrowing distally to an upwardly bent cylindrical neck with a wide circular thickened aperture with broadly everted rim. Immature female gonophore with several ova, reduced to one large planula at maturity.

Perisarc of stems thick, translucent white when young, becoming pale-straw coloured with age; gonotheca brown, female gonophore cream.

Monotheca australis, measurements (μm)

Hydrorhiza, width	~ 289
Stem	
length of internode	230–260
width at node	20–40
width at level of apophysis	90–149
Hydrocladium	
length of athecate internode	50–110
length of thecate internode	140–200
Hydrotheca	
diagonal length, margin to base	160–172
depth, margin to floor	90–180
diameter of rim	80–140
Nematotheca	
total length of median inferior	30–60
length of lateral including base	40–60
width of cup	20–50
width of axillar pore	14–20
Gonotheca	
length, including pedicel	650–1000
maximum width	200–350
diameter of neck	100–220
diameter of aperture	110–250

Remarks. The material in the dry Kirchenpauer collection of Museum Victoria is probably that on which Kirchenpauer (1876) described *Plumularia* (*Monopyxis*) *obliqua* var. *australis*. The specimen (NMV F58239) comprises many stems, some fertile, on dried leaves of the seagrass *Amphibolis antarctica*, formerly known as *Zostera*. Stranks (1993) nominated this material as possible syntype. Because of its unusual hydrocladial median inferior nematotheca, Bale (1884) raised Kirchenpauer's var. *australis* to specific rank as *Plumularia australis*. I designate F58239 as lectotype of *Monotheca australis* Kirchenpauer, 1876.

Compared with the height of the stems, the hydrorhizal stolons of *M. australis* are very wide, the strongly developed flexion joints permitting movement of the hydrorhiza on the *Amphibolis* leaves in strong water movement. Although the nematothecae are all essentially bithalamic, in some colonies the cup of the hydrocladial median inferior nematotheca is so adcaudally reduced that the line of demarcation between peduncle and cup is either very faint or altogether lost.

The small hydrostatic pore on the apophysis of the stem is obscured by the axillar nematotheca and is only visible in cleared specimens. The pore was described by Mulder and Trebilcock (1916) as similar in shape to a 'steamship ventilator'; in fresh material, however, it is cylindrical and likely to bend under pressure of a cover slip.

Monotheca australis is an obligate epiphyte of seagrasses, growing on *Amphibolis antarctica* in cool temperate south-eastern Australia and on *Posidonia australis* in warm temperate waters of southern and south-western Australia. In the rigorous *Amphibolis* habitat, the hydroid colonises the inner, sheltered leaves of the seagrass, while in the quieter *Posidonia* habitat it occurs on all but the outermost leaves of the plants. Colony size and cauline dimensions of *M. australis* on *Amphibolis* are usually smaller than those on *Posidonia*.

Boero (1981a, 1984) reported an increase in cauline length and loss of the intrathecal septum in *M. obliqua* from *Posidonia* seagrasses with increasing depth and decreasing water movement in the Mediterranean Sea. Because *M. australis* also grows on *Posidonia* in southern Australia, specimens from *Posidonia* habitat from 0–25 m depth were examined to investigate whether the same relationship exists among Australian *Monotheca* seagrass epiphytes. No such gradient was found; any tendency to loss of the intrathecal septum probably being lost in the more rigorous Australian *Posidonia* habitat.

Type locality. Port Phillip, Australia.

Known distribution. South-eastern and southern Australia to depth of 25 m.

Status of *Monotheca compressa* (Bale, 1882), *Monotheca aurita* (Bale, 1888) and *Monotheca obesa* (Blackburn, 1938). Bale (1882) described *Plumularia compressa* from fertile material collected by Mr T. B. Smeaton at Robe, South Australia. (The gonotheca was figured in 1884). The collection in Museum Victoria contains three microslides labelled by Bale '*Plumularia compressa* Bale, 1884'. These are presumably from Bale's 1882 collection and relabelled in 1884. The

specimens are probably from the shallow water seagrass *Posidonia australis* common at Robe. As Bale did not designate a holotype I designate a microslide NMV F59056 of a fertile colony as lectotype of *Monothecha compressa*.

Bale (1884, 1888, 1894) recognised the close relationship between *M. compressa* and *M. australis*, but nevertheless kept the two species separate — the main points of difference were length of stem, height and shape of the hydrotheca, position of the intrathecal septum and minor differences in shape of the neck of the gonotheca. Length of stem is an unreliable character as it may vary considerably between the same or different colonies according to environmental conditions and rate of growth. Height of the hydrotheca is quite variable over the range of material examined in the present study and is actually related to the degree of torsion around the intrathecal septum; shape of the base of the hydrotheca is also quite variable, some *australis* morphotypes being almost hemispherical in shape. The position of the foramen in the floor of the hydrotheca is also variable and depends on the degree of torsion of the hydrotheca around the intrathecal septum. It is more or less central in 75% of the *australis* morphotypes examined but is displaced towards the rear in the *compressa* form. Hydrothecae with a long, backwardly curved septum typical of Kirchenpauer's *australis* occur in colonies from the cool temperate *Amphibolis antarctica* habitat, the septum in these hydrothecae penetrating at least halfway into the hydrotheca, providing a pivotal point for torsion of the hydrotheca. In the warm temperate *Posidonia* habitat, the hydrothecae are taller and the septum is often directed forward as a rudimentary intrathecal ridge rather than a deep inflexion. Gonothecae vary in size and shape from almost cylindrical to turgid, and no relationship between sexual dimorphism, habitat or geographical distribution could be found to account for these variations.

Bale (1888) described *Plumularia aurita* from Botany, New South Wales. A microslide (NMV F58776) in the collection of Museum Victoria is the only known material of the species and was nominated syntype by Stranks (1993). As this is the only known specimen, by monotypy it is the holotype of the species. Bale's description and figure of the hydrotheca of *M. aurita* shows no intrathecal ridge, yet examination of the microslide clearly shows a backwardly oblique ridge passing almost halfway into hydrotheca. The incipiently monothalamic hydrocladial median inferior nematotheca is the same as that of *M. australis*, and the single small gonotheca on the slide although somewhat damaged confirms the species as a morphotype of *M. australis*. Although Bale provided no ecological notes, the species was almost certainly collected from *Posidonia* seagrass in Botany Bay.

The holotype microslide of *Plumularia obesa* Blackburn, 1938, in the collection of Museum Victoria, consists of three small, infertile stems labelled 'holotype NMV F70661, *Plumularia obesa* Blackburn, 1938, Reevesby Island, South Australia, December, 1936'. No other mounted or preserved material is known to exist. Since the microslide specimen was not cleared of tissue before mounting many critical structures are obscured, making it difficult to accurately measure important features.

In his description of *Plumularia obesa*, Blackburn surprisingly compared the species with *Plumularia spinulosa* rather than comparing it with *Plumularia australis*, which he also recorded from the same locality. The hydrotheca of *Monothecha obesa* closely resembles the *compressa* form of *M. australis* from *Posidonia* seagrass, the major difference being the shorter and more robust hydrocaulus resembling Bale's *M. aurita*. Blackburn described and figured the nematothecae of *P. obesa* as bithalamic with slender bases; however, examination of the type shows that the hydrocladial median inferior nematothecae have sturdy bases similar to those of *P. australis*. The bases of the twin lateral nematothecae are not slender as figured by Blackburn, nor are the cauline nematothecae of the holotype similar to the laterals and the bases are not so slender as to be considered truly moveable. Apart from the much smaller and more robust hydrocaulus, and taller hydrothecae, *P. obesa* is indistinguishable from the extreme *compressa* form of *M. australis*. Although the gonosome of *P. obesa* is unknown, I am confident that the species is a morphological variant of *M. australis* and, accordingly, I include it in the synonymy of *M. australis*.

Monothecha australis is a highly variable species, the size of the colony and structural dimensions over the geographic range are closely related to substrate type and environmental conditions.

Monothecha flexuosa (Bale, 1894)

Fig. 2 A–G

Plumularia flexuosa Bale, 1894: 115, pl. 5, figs 6–10.— Bartlett, 1907: 42.— Shepherd and Watson, 1970: 140.— Watson, 1973: 187.— Watson, 1982: 106, fig. 4.11e.— Watson, 1992: 220.— Stranks, 1993: 10.

?*Plumularia flexuosa*.— Bedot, 1921: 27.— Blackburn, 1938: 315.

Monothecha flexuosa.— Stechow, 1921: 260.— Stechow, 1925: 246.— Hirohito 1974: 37, fig. 17.— Watson, 1996: 78.— Watson, 2000: 48, fig. 37A, B.— Vervoort and Watson, 2003: 369.— Watson, 2003: 252.— Watson, 2005: 540.— Bouillon et al., 2006: 368.

Monothecha pulchella.— Medel and Vervoort, 1995: 58, fig. 25.— Medel and López-González, 1996: 202.— Watson and McInnes, 1999: 111.— Vervoort and Watson, 2003: 369, 373, fig. 90J–L.— Bouillon et al., 2004: 172, fig. 92G–K.

Material examined. Microslides in the Bale collection, Museum Victoria, labelled in Bale's handwriting are: NMV F58754, 'Catalogue number 206, *Plumularia flexuosa*, mouth of Snowy River, Dr Macgillivray, 1889' and three other slides, NMV F58755, all labelled '*Plumularia flexuosa*, Snowy River, Dr Macgillivray, 1892' (Bale's catalogue number 205).

Material in author's collection: Popes Eye reef, Port Phillip, fertile colonies on invertebrate and algal substrates, coll: J. Watson, depth 10 m, 20 September 2008. St Leonards pier, Port Phillip, depth 3 m, infertile colonies on red alga, coll: J. Watson, 10 August 2008. Clifton Springs, Port Phillip, jetty piles, depth 1.5 m, fertile colonies on algae, coll: J. Watson, 30 November 2005. Clifton Springs, Port Phillip, jetty piles, depth 1 m, fertile colonies on green alga *Caulerpa scalpelliformis*, coll: J. Watson, 16 September 2006. Clifton Springs, Port Phillip, jetty piles, depth 1.5 m, fertile colonies on green alga *Caulerpa scalpelliformis*, coll: J. Watson, 23 October 2008. Pearson Island, South Australia, infertile stems on red alga *Mychodea carnosa*, depth 37–45 m, coll: J. Watson, January 1969. Channel Island, Darwin, Northern Territory, depth 6 m, coll: J. Watson, July 2006.

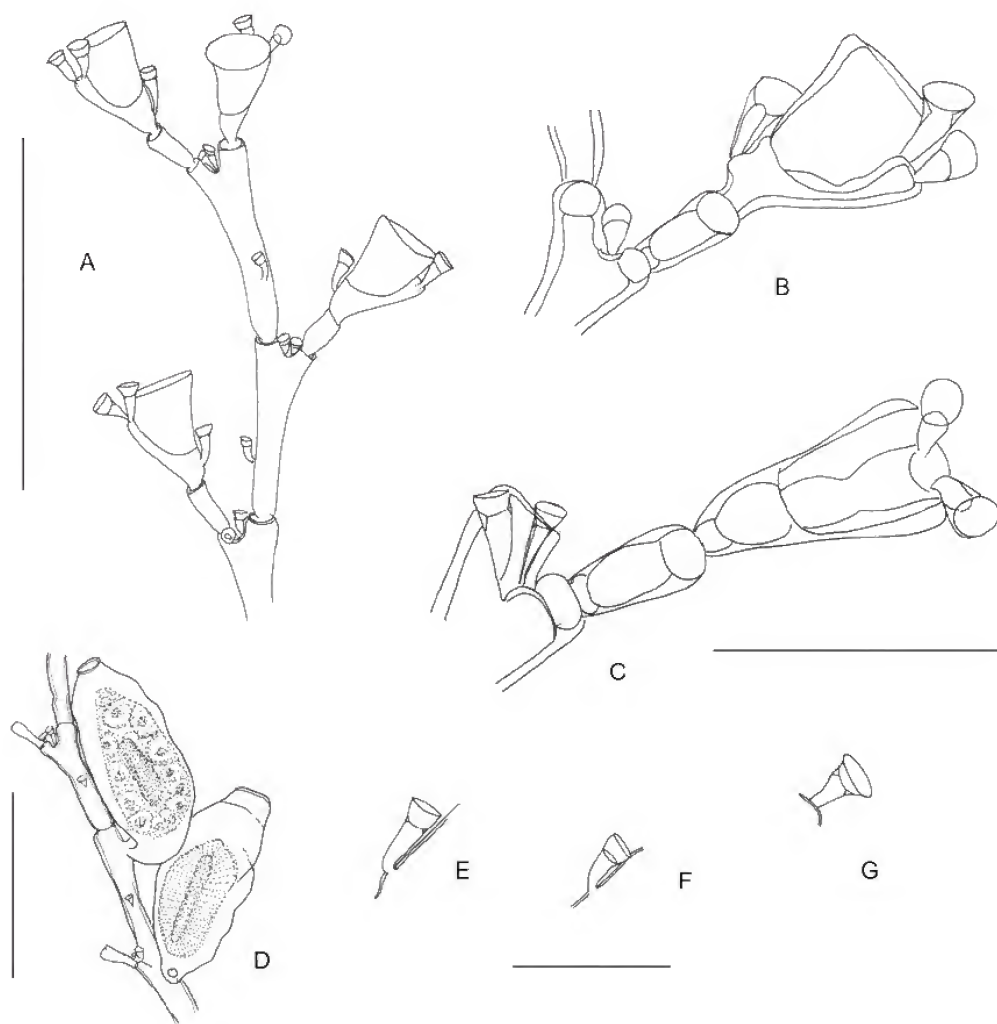


Figure 2. A–G, *Monothecha flexuosa*. A, part of stem; B, hydrocladium, lateral view; C, hydrocladium, ventral view; D, male and female gonothecae on same stem; E, median inferior nematotheca; F, cauline nematotheca; G, one of twin lateral nematothecae. Scale bar: A, D, 0.5 mm; B, C, 0.2 mm; E–G, 0.1 mm.

Description. Hydrorhiza of thin tubular stolons reptant on invertebrate substrate, sometimes intersecting in tangled knots, on algal substrate stolons often flattened with flexion joints. Caulus of same diameter as stolon, monosiphonic, flexuous, variable in length, up to 20 mm, base of stem smooth with a few irregular transverse joints; short stems unbranched, some longer stems with one or two orders of short side branches, stem internodes long.

Hydrocladia alternate, in one plane, borne on a strong apophysis below cauline node, apophysis curving smoothly away from internode, distal node transverse with rounded shoulder. Hydrocladial athecate internode long, cylindrical, straight to slightly curved, walls smooth, increasing slightly in

diameter distally; distal node transverse, deep, a transverse septum behind node, typically several transverse internal septa in internode.

Hydrothecate internode about same length as athecate internode, almost entirely occupied by hydrotheca, proximal node narrow, deep, inserted into shoulder of athecate internode; internode slightly distally inflated, terminating behind margin of hydrotheca, a faint intranodal septum sometimes in internode below hydrotheca. Hydrotheca cup shaped, adcauline wall convex, set deeply into internode, abcauline wall weakly concave, margin circular, transverse to hydrothecal axis, rim delicate, a slight thickening below margin.

Nematothecae all of same size and shape, bithalamic, moveable, fairly robust, base long, cup circular, slightly adcaudally shortened, three nematothecae on cauline internode, one on apophysis, the other axillar and one, variable in position, about one-third to mid-distance up internode, hydrocladial median inferior reaching one-quarter distance along hydrotheca, twin laterals extending well beyond rim of hydrotheca.

Gonothecae of both sexes borne thickly in a single row along lower stem or sparsely along branches. Male and female gonothecae the same shape, top-shaped when young, ovoid to barrel shaped at maturity, distally truncate, pedicel inserted beside apophysis of stem, upwardly bent, tapering into base of gonotheca; walls smooth to faintly undulated, aperture distal, transverse, circular, produced into a short thick neck of variable height closed by a low dome or shallow concavity. Male gonophore with rod-shaped spadix, mature female packed with large ova.

Cnidome:

- i) large microbasic euryteles capsule bean shaped 15–16 × 6 μm , abundant in coenosarc and nematothecae; discharges sideways.
- ii) small trisorhizas, capsule elongate, 5–7 × 2 μm , tubule short; abundant in coenosarc and tentacles.

Perisarc of hydrocaulus and gonothecae fairly thin, thicker at base of stems. Colonies transparent white, basal stem region brown in older colonies, male gonophores white, often with a shining bluish tinge, mature ova in female gonophore yellow.

Monotheca flexuosa, measurements (μm)

Hydrorhiza, width	50–80
Stem	
internode length	344–400
diameter at node	36–44
length of apophysis (adcauline wall)	48–52
Hydrocladium	
length of athecate internode	116–128
width at distal node (shoulder)	50–58
length of thecate internode (measured along base)	164–200
Hydrotheca	
length of abcauline wall	132–148
length of adcauline wall	136–60
diameter of margin	140–152
Gonotheca	
length (excluding pedicel)	560–696
maximum diameter	280–320
Nematotheca	
length of base	45–55
diameter of cup	40–50

Remarks. All microslides of *Monotheca flexuosa* in the Bale collection of Museum Victoria are designated syntypes by Stranks (1993). I designate NMV F58754 as lectotype of *Monotheca flexuosa*.

The systematic importance of the presence, absence or position of the cauline nematotheca has been much discussed by authors (e.g. Medel and Vervoort, 1995). In many southern Australian specimens of *M. flexuosa*, cauline nematothecae are present in the proximal one-third to mid-cauline internode, suggesting precise position is of little or no diagnostic value for identification of the species.

Stems of *M. flexuosa* from sheltered habitat are usually much longer, and more flexuous and silky in appearance than those from more rigorous habitats. The longer stems may bear a single row of up to 15 female gonothecae whereas shorter stems have fewer gonothecae, usually near the base of the stem. No correlation with environmental conditions or habitat could be found to explain the presence, absence or length of the terminal neck of the gonotheca.

M. flexuosa is the most abundant and widespread species of *Monotheca* in Australia. In southern Australia, it is fertile from late spring to autumn (November to March) when colonies occur on many invertebrate substrates (mussels, ascidians, polychaete tubes), on some flabellate red algae and the green algae *Caulerpa scalpelliformis* and *Caulerpa remotifolia*.

An unusual endoparasitic association between *M. flexuosa* and the red alga *Mychodea carnosus* was reported by Watson (1973). The stolons of the hydroid penetrate the outer medulla of young *Mychodea* fronds, producing external hydrocauli at intervals. As the alga grows, its tissue is gradually broken down by the hydroid stolons so that eventually the alga is attached to the substrate only by the hydrorhiza of the hydroid. Hydrocauli emerging from the algal medulla differ somewhat from the normal epiphytic form, comprising one or two short cylindrical basal internodes bearing one or two large nematothecae, followed by normal hydrocauline internodes.

Type locality. Mouth of Snowy River, Victoria, Australia.

Known distribution. Temperate and tropical Australia, New Zealand, Strait of Gibraltar. The species may prove to be cosmopolitan.

Monotheca hyalina (Bale, 1882)

Fig. 3A–I

Plumularia hyalina Bale, 1882: 41, pl. 15, fig. 9.— Bale, 1884: 141, pl. 12, figs 4, 5.— Bartlett, 1907: 422.— Bedot, 1921: 28.— Trebilcock, 1928: 24, pl. 6, fig. 6.— Watson, 1975: 170, fig. 29.— Stranks, 1993: 11.

Monotheca hyalina.— Stechow, 1921: 260.— Watson, 1996: 78.— Watson, 1997: 529.— Bouillon et al., 2006: 368.

Not *Plumularia hyalina*.— Ralph, 1961b: 41, fig. 5a, b.— Ralph, 1961c: 109.

Not *Monotheca hyalina*.— Vervoort and Watson, 2003: 371, fig. 90F–I.

Material examined. NMV F59052, microslide; NMV F59053, microslide, Bale collection, Museum Victoria, locality Queenscliff, Victoria.

Material in author's collection: Houtman Abrolhos Islands, Western Australia, infertile colony on *Sargassum* and red alga, depth 6–10 m, coll: J. Watson, 12 October 1986; Hopetoun, Western Australia, female colony on brown alga, depth 2 m, under ledge, coll: J. Watson, 13 January 1986. Boatswains Rocks, South Australia,

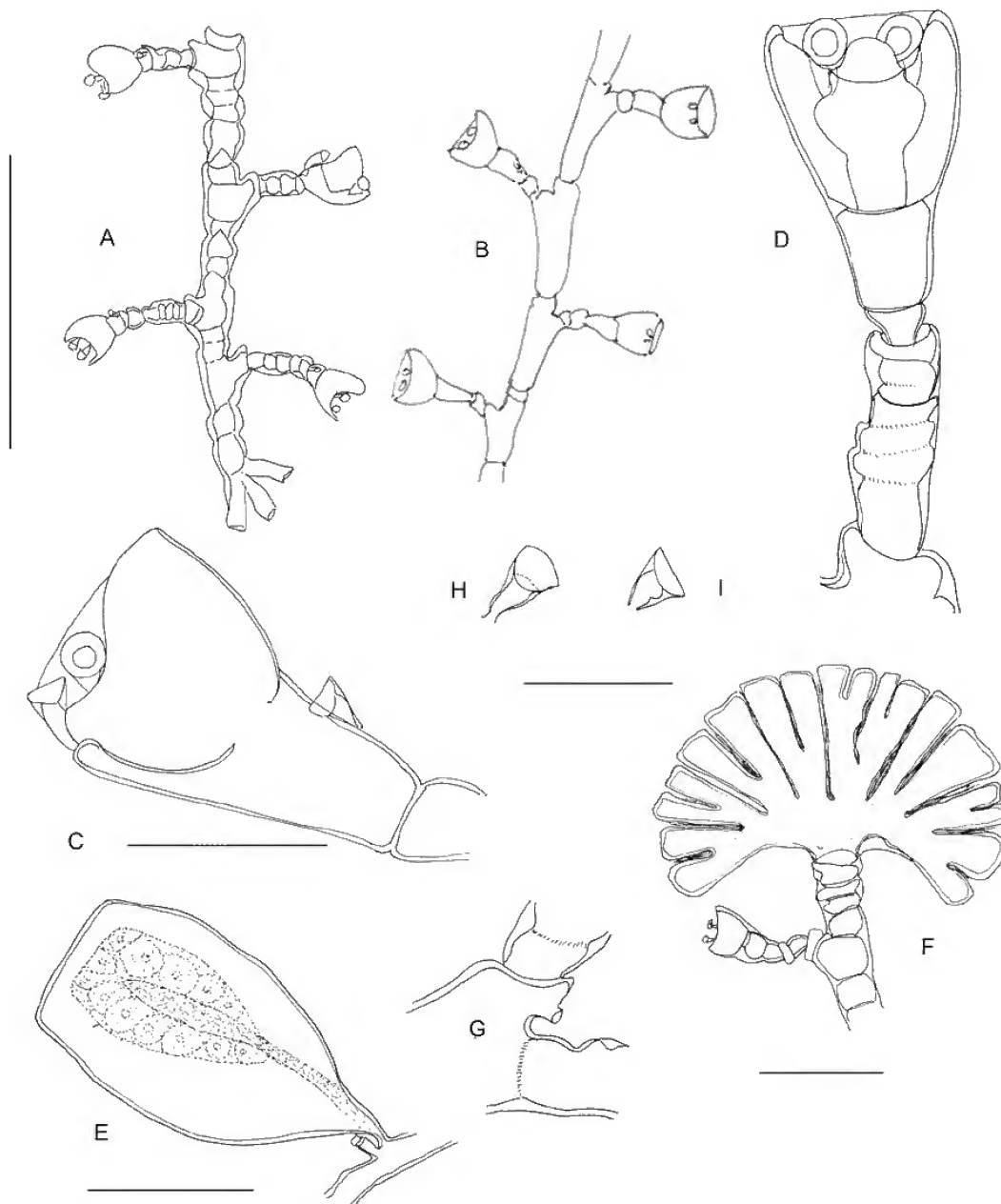


Figure 3. A–H, *Monotheca hyalina*. A, part of robust stem from cool temperate waters with intranodal septa; B, part of slender stem from temperate waters with no intranodal septa; C, hydrocladium and hydrotheca, lateral view; D, hydrocladium and hydrotheca, ventral view; E, gonotheca with female gonophore; F, apical stolonal plate; G, axillar hydrostatic pore; H, median inferior nematotheca; I, one of twin lateral nematothecae. Scale bar: A, B, 1 mm; C, D, 0.2 mm; E, 0.5 mm; G–I, 0.1 mm.

colony detached from substrate, coll: J. Watson, 27 January 1969. Fluted Cape, Bruny Island, Tasmania, female colony, depth 16 m, on red alga, coll: J. Watson, 10 February 1972. Lawrence Rocks, Portland, Victoria, infertile colony on red alga, depth 16 m, coll: J. Watson, 14 May 1969. Walkerville, Victoria, infertile colony detached from substrate, depth 3 m, coll: J. Watson, 1 March 1968. Nambucca Heads, New South Wales, infertile colony on coralline alga and ascidian, depth 13 m, coll: J. Watson, 11 January 1972.

Description. Hydrorhiza of tubular rugose stolons reptant on substrate; stolons usually with internal flexion joints. Stems 3–10 mm high, monosiphonic, straight to weakly sympodial, up to four short basal internodes with transverse joints above hydrorhiza. Succeeding stem internodes variable in length, longer ones typically on taller stems, smooth, expanding a little distally with a strong oblique V-shaped proximal node and a transverse distal node, usually an internal transverse septum below distal node at level of apophysis.

Shorter stems with one, rarely two, short proximal athecate internodes, stem thereafter hydrocladate; cauline internodes deeply and more or less irregularly septate with strong V-shaped proximal nodes and transverse distal nodes, and three or four strong transverse internal septa. Hydrocladia alternate, fairly long, given off in one plane from a short, strong apophysis distal on internode, apophysis curving smoothly out from internode, adcauline wall a shoulder with slightly oblique deep node, a cylindrical axillar hydrostatic pore on adcauline shoulder.

Athecate hydrocladial internode long, deeply inserted in shoulder of apophysis, with deep transverse distal node and several complete internal septa. Hydrothecate internode longer than athecate internode, terminating in a protuberance separating the twin lateral nematothecae, hydrotheca set deeply in internode, a large prehydrothecal chamber expanding from proximal node to floor of hydrotheca; hydrotheca deep bowl shaped, base convex with a large foramen connecting with prehydrothecal chamber; in lateral view abcauline wall convex, adcauline wall completely adnate to internode, in ventral view walls expanding in a smooth curve from base, narrowing just below margin, rim slightly thickened but not everted; margin hemispherical, wide in ventral view, abcauline side straight, adcauline side deeply concave, in lateral view, wall a broad sinuous curve down to internode.

Three nematothecae on hydrothecate internode, hydrocladial median inferior about halfway along prehydrothecal chamber, small, bithalamic, moveable, adpressed to internode, base tapering, cup slightly adcaudally shortened, twin laterals of same shape as median, standing erect on each side of strong terminal protuberance of internode, tucked within hydrothecal margin, cup circular to slightly laterally compressed but not excavated; no cauline nematothecae.

Gonotheca large, one to several in a row on lower stem, conical, widening from a short indefinite pedicel inserted beside apophysis, walls of gonotheca smooth to obscurely undulated, truncated distally by a transverse, weakly concave aperture without operculum; female gonophore with 15–20 large ova.

Perisarc of slender stems thin, much thicker in shorter, robust stems.

Colour of live colonies where known, buff to yellow, gonophores yellow.

***Monotheca hyalina*, measurements (µm)**

	Slender group (warm temperate)	Robust group (cool temperate)
Hydrorhiza, width	112–120	88
Stem		
length of internode	456–640	304–400
width at node	80–120	80–112
distal width of apophysis	80–100	92–112
Hydrocladium		
length of athecate internode	80–220	80–120
length of hydrothecate internode	200–296	184–212
Hydrotheca		
length of abcauline wall	193–220	152–160
length of adcauline wall	160–186	80–116
width of margin front view	160–192	128–168
Nematotheca		
basal length of median inferior	35–42	16–26
diameter of cup	42–52	40–60
basal length of lateral	40–50	30–40
diameter of cup	40–46	44–50
Gonotheca		
length, including pedicel	960–1400	920
maximum width (margin)	720–900	680

Remarks. There is no known type material of *Monotheca hyalina*; a microslide NMV F59052 in the Museum Victoria Bale collection labelled in Bale's handwriting '*Plumularia hyalina* Queenscliff, February 1881' was nominated as probable syntype by Stranks (1993). I select this microslide as lectotype of *Monotheca hyalina*.

Monotheca hyalina is very variable in height of the stem, and slenderness and robustness of the hydrocaulus, in the presence or absence of intranodal septa and size of the hydrotheca. In some specimens, the prehydrothecal chamber is so reduced that the hydrocladial median inferior nematotheca extends one-third the length of the hydrotheca.

Specimens from warm-temperate southern Australian

waters are distinguished by their slender, flexuous stems with longer internodes, while those from the cool-temperate waters have sturdier stems with shorter internodes and smaller hydrothecae. Dimensions of these two groups are compared in the above table.

Despite the considerable structural and dimensional differences between the two morphological extremes, intergradation does occur, hence *M. hyalina* is recognised as a single but somewhat variable species. It is often difficult to obtain a good lateral view of the hydrotheca as they tend to twist forward in microslide preparations. *M. hyalina* is an algal epiphyte; some specimens have a large apical stolonal plate to securely anchor stems in a rigorous oceanic environment.

Examination of New Zealand material and a review of descriptions of Ralph (1961b) and Vervoort and Watson (2003) suggests that the New Zealand material is not *M. hyalina* because: i) the hydrotheca is pitcher-shaped with a short, concave free adcauline wall, ii) there is a partial intranodal septum below the hydrotheca, iii) there is an axillar nematotheca in the apophysis of the stem, and iv) as the New Zealand specimens usually have more than one hydrotheca on the hydrocladium it is excluded from *Monotheca* as defined here. It is likely that the New Zealand material is an undescribed species of *Plumularia*. It is noteworthy that Leclère et al. (2007) in their molecular analysis demonstrate that *M. hyalina* from New Zealand is outside the group, thus supporting the conclusion that the New Zealand species is not *M. hyalina*.

Type locality. Queenscliff, Victoria, Australia.

Known distribution. Southern Australia.

Monotheca obliqua (Johnston, 1847)

Fig. 4 A–E

Plumularia obliqua Johnston, 1847: 106, pl. 28, fig. 1.— Bale, 1884: 138, pl. 12, figs 1–3.— Bartlett, 1907: 43.— Mulder and Trebilcock, 1910: 116.— Mulder and Trebilcock, 1916: 76, pl. 11, figs 1–1e.— Jäderholm, 1919: 22, pl. 5, fig. 6.— Stechow, 1919: 113.— Bedot, 1921: 28.— Billard, 1927: 342.— Broch, 1933: 31, fig.— Leloup, 1934: 15.— Billard, 1936: 9.— Blackburn, 1938: 315.— Blackburn, 1942: 108.— Hodgson, 1950: 39, fig. 68.— Rossi, 1950: 23, fig. 4b.— Pennycuik 1959: 180.— Watson, 1973: 189.— Millard and Bouillon, 1974: 9, 34, fig. 8A–D.— Millard, 1975: 396, fig. 125A–B.— García-Corralles, Aguirre Inchaurre and Gonzalez Mora, 1978: 56, fig. 25.— Millard, 1978: 196 et seq.— Watson, 1979: 234.— Boero, 1981a: 197.— Hirohito, 1983: 69.— Boero, 1984: 103, fig. 8.— Boero et al., 1985: 29.— Gili and García-Rubies, 1985: 48, fig. 5B.— Isasi and Saiz, 1986: 70.— Roca, 1987: 151.— Gili, Vervoort and Pagès, 1989: 89, fig. 17A.— Boero and Bouillon, 1989: 39, fig. 1. García Rubies, 1992: 265.— Park, 1992: 294. Cornelius, 1995: 142, fig. 33.— Bouillon et al., 1995: 61.— Hirohito, 1995: 275, fig. 94d–f.— Watson and McInnes, 1999: 111.— Bouillon et al., 2006: 368.

Monotheca obliqua.— Stechow, 1923b: 17.— Leloup, 1932: 160.— Yamada, 1959: 78.— Rho and Park, 1986: 99.— Ryland and Gibbons, 1991: 538, fig. 9.— El Beshbeeshy, 1995: 404.— Medel and López-González, 1996: 202.— Watson, 1973: 529.— Watson and McInnes, 1999: 111.— Vervoort and Watson, 2003: 369.— Watson, 2005: 541, fig. 15.— Bouillon et al., 2006: 368.

Plumularia (Monotheca) obliqua.— Stechow and Uchida, 1931: 565.

Plumularia obliqua australis.— Stranks, 1993: 8.

Material examined. NMV F101686, infertile colony, New Island, Archipelago of the Recherche, Western Australia, depth 20 m on red alga, coll: J. Watson, February 2003. WAM Z29970, fertile colony, New Island, Archipelago of the Recherche, Western Australia, depth 20 m, on brown alga, coll: J. Watson, February 2003.

Material in author's collection: fertile colony, Popes Eye reef, Port Phillip, Victoria, on stem of *Macrorhynchia whiteleggei*, depth 6 m, coll: J. Watson, 7 November 2009. Infertile colony, Popes Eye reef, Port Phillip, Victoria, depth, 3 m, on thallus of *Sargassum* sp., coll: J. Watson 29 December 2009.

Description. Hydorhiza reptant on substrate, tubular, somewhat rugose. Stems to 7 mm long, monosiphonic, straight to sympodial, internodes moderately long, widening to distal node; node transverse to slightly oblique, often a distinct shoulder in perisarc and an internal septum above, sometimes one to three strong internal septa in proximal part of internode. Apophysis of stem short, upwardly directed, situated well below node, widening to a strong distal shoulder.

Hydrocladia alternate, short, in one plane, distal on internode, athecate internode with one to three internal septa, distal node transverse. Hydrothecate internode almost completely occupied by hydrotheca, internode with one or two faint septa below hydrotheca, sometimes a short, faint septum passing into hydrotheca from distal septum; internode distally inflated, pushing base of hydrotheca upward, prehydrothecal chamber short, triangular with internal triangular septum.

Hydrotheca scoop shaped, abcauline and adcauline walls smoothly convex, margin cut obliquely back to internode, rim slightly everted, a thickening behind rim.

Cauline and hydrocladial median inferior nematothecae similar in shape and size, bithalamic, moveable, base moderately long, cup fairly wide, cauline nematotheca about one-third distance up internode on side opposite hydrocladium, standing out from internode, base connecting with a large foramen of internode, hydrocladial median inferior nematotheca adpressed to prehydrothecal chamber, just reaching floor of hydrotheca; twin laterals directed outwards from an indentation in distal protuberance of internode, base short, stout, cup deeply adcaudally excavated; a nematotheca in axil beside apophysis; a dome-shaped axillar hydrostatic pore with small terminal aperture, sometimes also a small secondary pore on adcauline shoulder of apophysis.

Male and female gonothecae borne on the same colony but not on same stems, of same shape and size, large, conical, circular in section, perisarc fairly thick with tendency to proximal rugosity, typically one borne on a short, thin pedicel beside an apophysis near base of stem; aperture transversely truncate, occupying entire width of gonotheca, closed by a sheet of tissue. Female gonophore containing many large ova.

Perisarc of stems pale brown basally, becoming colourless distally, gonotheca pale brown, gonophores flesh-coloured.

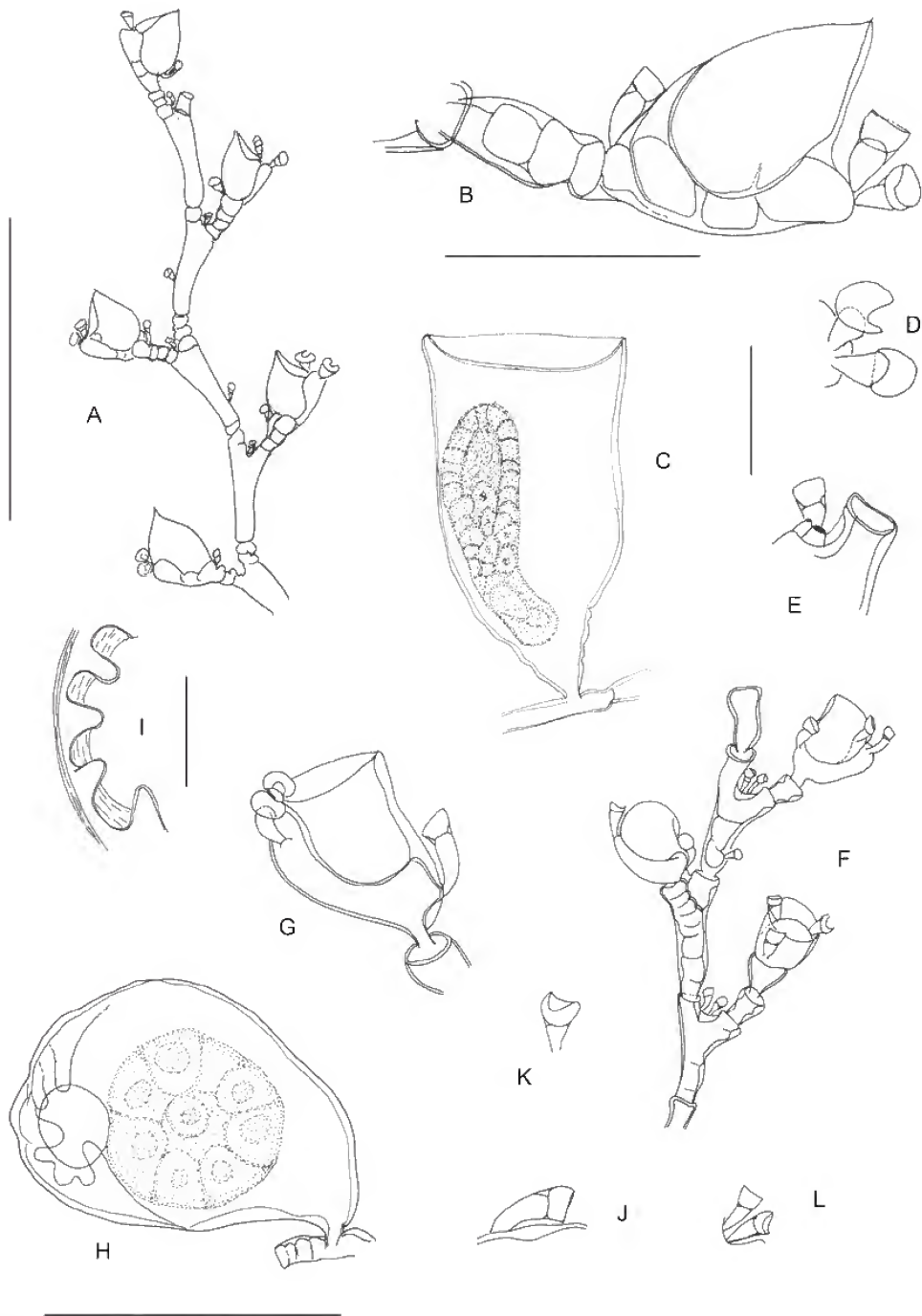


Figure 4. A–E, *Monotheca obliqua*. A, part of stem; B, hydrocladium and hydrotheca; C, female gonotheca; D, twin lateral nematothecae; E, axillar nematotheca and hydrostatic pore. Scale bar: A, C, 1 mm; B, 0.2 mm; D, E, 0.1 mm. F–L, *Monotheca pulchella*. F, part of stem; G, hydrocladium and hydrotheca; H, female gonotheca with ova; I, anterior view of gonothecal aperture with internal lobate submarginal cusps; J, median inferior hydrocladial nematotheca; K, one of twin lateral nematothecae; L, axillar nematothecae. Scale bar: A, C, 1 mm.; B, 0.2 mm; F, H, 0.5 mm; D–E, I–L, 0.1 mm.

***Monotheca obliqua*, measurements (µm)**

Hydrorhiza, width	70–88
Stem	
length of internode	200–320
width at distal node	40–60
Apophysis	
length of adcauline wall	26–58
width at distal shoulder (node)	40–70
Hydrocladium	
length of athecate internode	56–80
width at distal node	42–60
length of thecate internode	160–104
Hydrotheca	
length of abcauline wall	140–200
length of of adcauline wall	80–148
depth, floor to margin tip	180–200
width at rim	160–180
Nematotheca	
total length of lateral	52–60
diameter of cup	42–48
length of median	48–52
diameter of cup	26–28
Gonotheca	
length, including pedicel	1240–1580
width at margin	640–1100

Remarks. *Monotheca obliqua* is a well-known species with worldwide distribution. Mulder and Trebilcock (1910, 1916) briefly described material collected from Bream Creek on the Bass Strait coast and Corio Bay in Port Phillip, commenting on the slenderness of the base of the median inferior nematotheca, the small axillar hydrostatic pore and the abcauline flange connecting the base (prehydrothecal chamber) of the hydrotheca to the internode.

Although widely distributed across the south and east of the continent, *M. obliqua* is not a common species in Australia.

Type locality. British Isles.

Known distribution. Cosmopolitan; southern Australia to Queensland.

***Monotheca pulchella* (Bale, 1882)**

Fig. 4 F–L

Plumularia pulchella Bale, 1882: 30, pl. 15, figs 6, 6a.— Bartlett, 1907: 43.— Stranks, 1993: 13. — Watson, 1994: 67.

Not *Plumularia pulchella*. — Bedot, 1921: 28.— Trebilcock, 1928: 24. — Totton, 1930: 221, fig. 58 a–d.— Hodgson, 1950: 41, fig. 71.— Ralph, 1961b: 39, fig. 5 c–e.— Blanco, 1973: 73, figs 1–3.— Millard, 1975: 398, fig. 125 C–D.— Izquierdo et al., 1986: 54, fig. 5.— Genzano, 1990: 50, figs. 16–17.— Medel and Vervoort, 1995: 58, fig. 25.— Vervoort and Watson, 2003: 369, 373, fig. 90J–L.— Bouillon, et al., 2004: 172, fig. 92G–K.

?*Plumularia pulchella*.— Blackburn, 1942: 108.— Day et al., 1952: 404.— Millard, 1957: 232.— Millard, 1962: 300.— Pennycuik, 1959: 180.— Ralph, 1961b: 109.— Millard, 1966: 493.— Berrisford, 1969: 394.— Day et al., 1970: 14.— Millard, 1978: 196.— Millard, 1980: 133.— Medel and López-González, 1996: 202.

Monotheca pulchella.— Stechow, 1921: 260.— Watson and McInnes, 1999: 111.

Material examined. NMV F59054, Bale collection, Museum Victoria, one microslide, labelled in Bale's handwriting 'Plumularia pulchella Bale, Queenscliff, November, 1878'.

Material in author's collection: microslide and preserved material, Knobbies Island, Western Port, on brown alga, coll: J. Watson, depth 10 m, 27 January 1985.

Description. Hydrorhiza flat and ribbon-like with flexion joints. Stems monosiphonic, straight to weakly sympodial, basal athecate region with several transverse nodes often with one or two nematothecae, succeeding cauline internodes variable in length, cylindrical, robust, nodes deep, transverse to oblique, internode typically with several internal septa imparting a wrinkled appearance to stem.

Hydrocladia alternate, usually in one plane, but sometimes one or two forwardly displaced, halfway to one-third distance up internode, apophysis of stem upwardly directed away from internode, long, stout, with a broad transverse distal shoulder, usually an internal septum behind shoulder; hydrocladium short, athecate internode variable in length, proximal end narrow, inserted into shoulder of apophysis. Hydrothecate internode variable in length, almost entirely occupied by hydrotheca, proximal end of internode a narrow neck inserted into athecate node; distal end terminating in a protuberance behind hydrothecal margin.

Hydrotheca cup shaped, adcauline wall convex, immersed in internode, abcauline wall weakly concave and thickened; margin circular, transverse.

Nematothecae bithalamic, moveable, cauline and hydrocladial median inferior of same size and shape, base long and conical, cup deep, rim circular, slightly adcaudally shortened; a nematotheca one-third distance up cauline internode and two axillar; hydrocladial median inferior seated on a prominence of internode, just reaching base of hydrotheca, twin laterals seated almost at end of internode, base fairly short, cup adcaudally excavated.

Male and female gonothecae borne on same stem. Sexes of same shape, kidney shaped to ovoid, inserted on a smooth, short, bent pedicel at base of apophysis, pedicel expanding and merging into body of gonotheca; walls of gonotheca thick, smooth to faintly rugose, aperture distal, circular, displaced to one side, rim slightly thickened, a submarginal row of large, irregularly shaped inwardly directed lobate cusps, usually one or two larger than the others. Mature female gonophore containing a large ovum.

***Monotheca pulchella*, measurements (μm)**

Stem	
internode length	204–400
diameter at node	48–60
length of apophysis (adcauline wall)	52–64
Hydrocladium	
length of athecate internode	52–128
width at distal node (shoulder)	50–58
basal length of hydrothecate internode	164–200
Hydrotheca	
length of abcauline wall	100–148
diameter of margin	116–152
Gonotheca	
length (excluding bent pedicel)	560–696
maximum width	280–344
Nematotheca	
length of base	40–55
diameter of cup	32–50

Remarks. Stranks (1993) considered microslide NMV F59054 a probable syntype of *Monotheca pulchella*. I select this microslide as lectotype of *Monotheca pulchella*.

The submarginal lobate cusps mentioned by Bale are clearly visible in the gonotheca of the type. On present evidence, *M. pulchella* is associated only with brown algae. This is in contrast to *M. flexuosa*, which is a common opportunistic species occurring on a wide variety of red and green algal and invertebrate substrates.

The hydroid reported as *Plumularia pulchella* by Izquierdo et al. (1986) from the Canary Islands is probably *Monotheca margareta* (see discussion in Calder, 1997), further supporting the contention that *M. pulchella* is endemic to Australia.

Type locality. Queenscliff, Victoria, Australia.

Known distribution. Victorian coastal waters.

Distinction between *Monotheca flexuosa* and *Monotheca pulchella*. *Monotheca pulchella* (Bale, 1882) has often been confused by authors with *Monotheca flexuosa* (Bale, 1894). Although Bale clearly distinguished between the two species on the basis of *M. pulchella* having a robust septate stem, very short cauline internodes and hydrocladia midway along the internode, Totton (1930) reported infertile material from northern New Zealand as *M. pulchella*, presumably following Trebilcock (1928), who synonymised *M. flexuosa* in that species. Totton's opinion was based on i) the specimens being twice the size of those described by Bale (for *M. flexuosa*), some being half an inch in height (12 mm) and bearing 48 hydrocladia, ii) the trophosome of *M. flexuosa* falling well within the range of variation of *M. pulchella* and iii) there being only slight apparent differences in the gonosome. His figure (fig. 58, p. 221) is clearly that of *M. flexuosa*.

Later authors, such as Millard (1975) followed Totton but, with the exception of Millard, they did not provide figures of their specimens so the accuracy of their identifications cannot

be confirmed. Watson (1973) examined Bale's microslide specimens of both species in the collection of Museum Victoria, reporting the species to be markedly different and concluded that Totton was incorrect for the following reasons: i) height of the hydrocaulus is an unreliable character, ii) *M. flexuosa* has a more flexuous hydrocaulus than *M. pulchella* and iii) the gonothecae of the two species are markedly different. Medel and Vervoort (1995) misinterpreted Watson's (1973) note on the submarginal gonothecal cusps of *M. pulchella*, and their description and figure is clearly that of *M. flexuosa*. Infertile material on green algae reported from New Zealand by Vervoort and Watson (2003) is also *M. flexuosa*.

On present evidence, *M. pulchella* is endemic to southern Australia where it is associated only with brown algae.

***Monotheca spinulosa* (Bale, 1882)**

Fig. 5A–G

Plumularia spinulosa Bale, 1882: 30, pl. 15, fig. 8.— Bale, 1884: 139, pl. 12, figs 11–12.— Bale, 1888: 783, pl. 19, figs 11–13.— Von Lendenfeld, 1885a: 475.— Bartlett, 1907: 43.— Warren, 1908: 320.— Mulder and Trebilcock, 1910: 123, pl. 3, fig. 9, 9a.— Mulder and Trebilcock, 1916: 81, pl. 11, fig. 4.— Briggs, 1918: 34, 43.— Bedot, 1921: 29.— Blackburn, 1937: 368.— Blackburn, 1942: 116.— Pennycook, 1959: 180.— Ralph, 1961: 109.— Millard, 1962: 301.— Millard, 1966: 494.— Berrisford, 1968: 394.— Day, et al., 1970: 14.— Watson, 1973: 188, figs 54, 55.— Millard, 1975: 401, fig. 125 E–J.— Millard, 1978: 196.— Watson, 1982: 107, fig. 4.11f–h.— Stranks 1993: 13.

Monotheca spinulosa.— Stechow, 1921: 260.— Stechow, 1923: 17.— Leloup, 1932: 160.— Millard, 1975: 401, fig. 125 E–J.— Millard, 1978: 196.— Hirohito, 1995: 278, fig. 96a–c.— Watson, 1996: 78.— Watson, 1997: 529.— Watson and McInnes, 1999: 111.— Watson 2003: 243, 252.— Vervoort and Watson, 2003: 369, 374.— Watson, 2005: 542.— Bouillon et al., 2006: 368.

Plumularia spinulosa var. *obtusa*.— Millard, 1957: 232.

Monotheca spinulosa var. *obtusa*.— Stechow, 1923d: 225.— Yamada, 1959: 78.

Material examined. NMV F59053, microslide, Queenscliff Victoria, Bale collection, Museum Victoria, nominated as probable syntype by Stranks (1993).

Material in author's collection: Stradbroke Island, south Queensland, on alga, depth 20 m, coll: J. Watson, 24 August 1975. Coniston Bay, Port Kembla, New South Wales, on bryozoan, depth 18 m, coll: J. Watson, September 1975. Gabo Island, Victoria, on ascidian *Herdmania grandis* and red algae under ledges, depth 12 m, coll: J. Watson, 15 February 1973. Port Phillip Heads, Victoria, on red alga, depth 10 m, coll: J. Watson, 9 January 1984. South (20 km) of Cape Bridgewater, Victoria, on red alga, depth 100 m, coll: V. Johnstone, from fishing trawl, 16 May 1969. Port Noarlunga, South Australia, on red alga, depth 10 m, coll: J. Watson, 10 February 1976. Abrolhos Islands, outer reef, Western Australia, on red alga, depth 15 m, coll: J. Watson, 17 October 1986. Karapuki Island, New Zealand, coll: D. A. Staples 14 September 1975 on red alga.

Description. Hydrorhizal stolons ribbon-like, flattened to substrate, outer flange with flexion joints in perisarc. Stems monosiphonic, to 5 mm high, basal stem region athecate, sometimes with two or three transverse nodes. Cauline internodes variable in length among colonies but typically moderately long and slender, straight to slightly curved, walls smooth, expanding slightly distally to apophysis, nodes

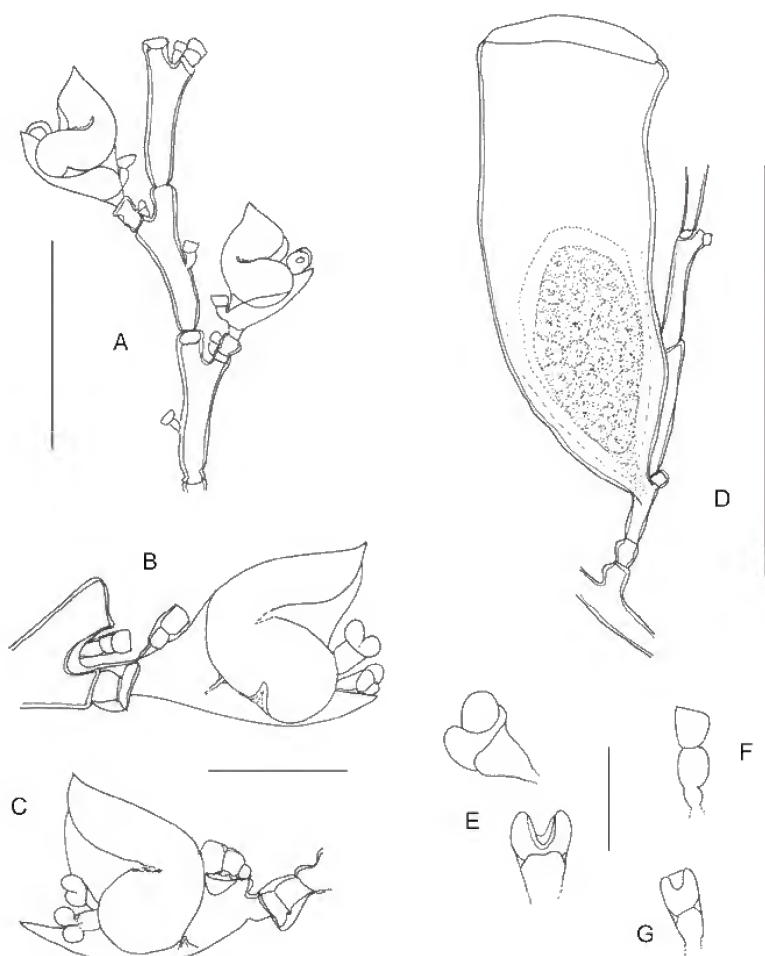


Figure 5. A–G, *Monotheca spinulosa*. A, part of stem; B, hydrocladium with short terminal spine; C, hydrocladium with long terminal spine; D, female gonotheca with ova; E, two views of twin lateral nematothecae; F, axillar nematotheca; G, median inferior nematotheca. Scale bar: A, 0.3 mm; B, C, 0.2 mm; D, 1 mm; E–H, 0.1 mm.

transverse to slightly oblique, deeply constricted, an internal transverse septum below node.

Hydrocladia alternate, distal on internode, in one plane, borne on an upwardly directed apophysis, abcauline wall of apophysis a smooth extension of internode, distal node a deep transverse shoulder with internal septum behind node, a minute mound-shaped hydrostatic pore in axil beside a nematotheca. Hydrocladium with a short proximal athecate internode, distal node transverse, deeply constricted with an internal septum, occasionally an identical secondary athecate internode between the athecate and hydrothecate internode. Hydrothecate internode narrow, short, ending in a distal spine of variable length, projecting beyond hydrotheca.

Hydrotheca occupying most of internode; internode expanding distally as a prehydrothecal chamber between node

and floor of hydrotheca, often a minute septum projecting backwards into chamber from floor of hydrotheca. Hydrotheca bonnet shaped, laterally compressed, adcauline wall rounded, set deep in internode, abcauline wall curved, proximally convex, straightening towards margin; margin delicate, deeply divided by a long V-shaped septum passing deeply backwards into hydrotheca, a minute triangular in septum in base of some hydrothecae. Hydranth with 12–14 tentacles.

Nematothecae bithalamic, moveable, all approximately of same size: one cauline, halfway along internode on opposite side to apophysis, one on internode in axil, one median inferior, base close to internode, twin laterals standing erect in front of hydrotheca, one at each side of distal spine, bases short, slightly inflated, cup deeply adcaudally excavated into a butterfly shape.

Male and female gonothecae large, one to several borne near base of stem, inserted on a short indistinct pedicel beside apophysis; body narrowly conical, facing upwards, walls smooth to weakly undulated, distally truncate, closed by a sheet of tissue, immature female gonophore with many ova.

Perisarc of stem and gonotheca moderately thick, thin on hydrothecal margin. Colonies colourless to white.

***Monothecha spinulosa*, measurements, (μm)**

Hydrorhiza, width	96–120
Stem	
internode length	228–320
diameter at node	30–50
length of apophysis (adcauline wall)	30–40
Hydrocladium	
length of athecate internode	32–56
width at distal node (shoulder)	40–60
length of base of thecate internode (excluding spine)	160–192
length of subhydrothecal chamber	199–200
length of terminal spine	18–64
Hydrotheca	
length of abcauline wall (measured diagonally from base)	156–200
width of margin	136–168
Gonotheca	
length (excluding pedicel)	1200–1560
maximum width (at margin)	640–740
Nematotheca	
length of base	22–32
diameter of cup	22–36

Remarks. A microslide (NMV F59053) in the Bale collection of Museum Victoria labelled '*Plumularia spinulosa* Bale 1882, Queenscliff' was nominated as a probable syntype by Stranks (1993). As this is the only known specimen, by monotypy it is the holotype of the species.

The position of the cauline nematotheca varies between colonies, typically being about halfway along the internode but sometimes only one-third the distance up from the proximal node. The position of the cauline apophysis is also somewhat variable, ranging from well below to close to the distal node. The axillar hydrostatic pore is very small and is only seen with careful searching.

Stechow (1923) erected the var. *obtusa* for morphotypes with a blunt terminal hydrocladial spine and Ralph (1961b) erected the var. *spinulosa* for material from New Zealand with a long terminal spine. Later studies, including the present one, suggest the length of the spine is very variable. Watson (2005) suggested it may be a response to environmental conditions and evidence from this study supports this conclusion, specimens with the longest spines being from deeper, less turbulent habitat.

M. spinulosa is a very small species with a preference for a substrate of flabellate red algae.

Type locality. Queenscliff, Victoria, Australia.

Known distribution. Temperate southern Australia to southeast Queensland, Lord Howe Island, New Zealand, Japan, South Africa, south Atlantic. Littoral to 100 m.

***Monothecha togata* (Watson, 1973)**

Fig. 6 A–I

Plumularia togata Watson, 1973: 191, figs 65–67.— Bouillon et al., 2006: 371.— Stranks, 1993: 14.

?*Monothecha togata*.— Vervoort and Watson, 2003: 374, fig. 91A–E.

Material examined. NMV F42060, holotype, microslide (malinol mounted), Pearson Island, South Australia, on red alga *Metagoniolithon charoides*, depth 33 m, coll: S. Shepherd 8 January 1969. Paratypes: microslides NMV F42061, F42062, F42063, F4G2064, F42065, F42066, F42105; SAMH40, Pearson Island on red alga *Metagoniolithon charoides*, coll: S. Shepherd, 8 January 1969.

Description. Hydrorhiza a network of broad, flat stolonal tubes with internal flexion joints. Stems short, to 4 mm long, monosiphonic, with one to three short basal internodes, nodes transverse, succeeding internodes moderately long and slender, expanding distally to a broad shoulder at apophysis, a strong transverse septum above and below node at level of apophysis, distal node V-shaped, sometimes a weak transverse septum about halfway up internode near level of cauline nematotheca.

Apophysis short, robust, just below distal cauline node, slightly frontal on stem, upwardly directed, abcauline wall a continuation of internode, adcauline wall set close to internode, distal end wide, thickened, node transverse, a weak oblique internal septum below node.

Hydrocladia alternate, one on cauline internode, slightly forwardly directed, athecate internode very short, corrugated, a strong transverse internal septum, distal node transverse. Hydrothecate internode much longer than athecate internode, inserted into shoulder of athecate internode with a slender V-shaped joint; internode downwardly curved below hydrotheca.

Hydrotheca cowl shaped (lateral view), scoop shaped (anterior view), with a distinctly peaked adcauline margin (i.e. opposite base of hydrotheca), prehydrothecal chamber short, inflated, upper (adcauline) wall strongly convex, sometimes a faint septum passing from internode into base, hydrothecal margin hemispherical to triangular (anterior view), in lateral view adcauline wall extending in a peak over margin; rim thickened and outrolled.

Nematothecae bithalamic, moveable, all similar in shape but differing slightly in length of base, cup robust, wide and fairly shallow, adcaudally excavated almost to base; one cauline, about halfway along internode on same side as apophysis, one axillar beside apophysis, one median inferior on hump of prehydrothecal chamber, just reaching base of hydrotheca, twin laterals standing close together at either side of a low distal protuberance of internode, bases short, sides facing inwards to hydrothecal margin; in lateral view, nematothecae appear to be almost inside hydrothecal margin.

Male gonotheca large, inserted on a short, straight pedicel

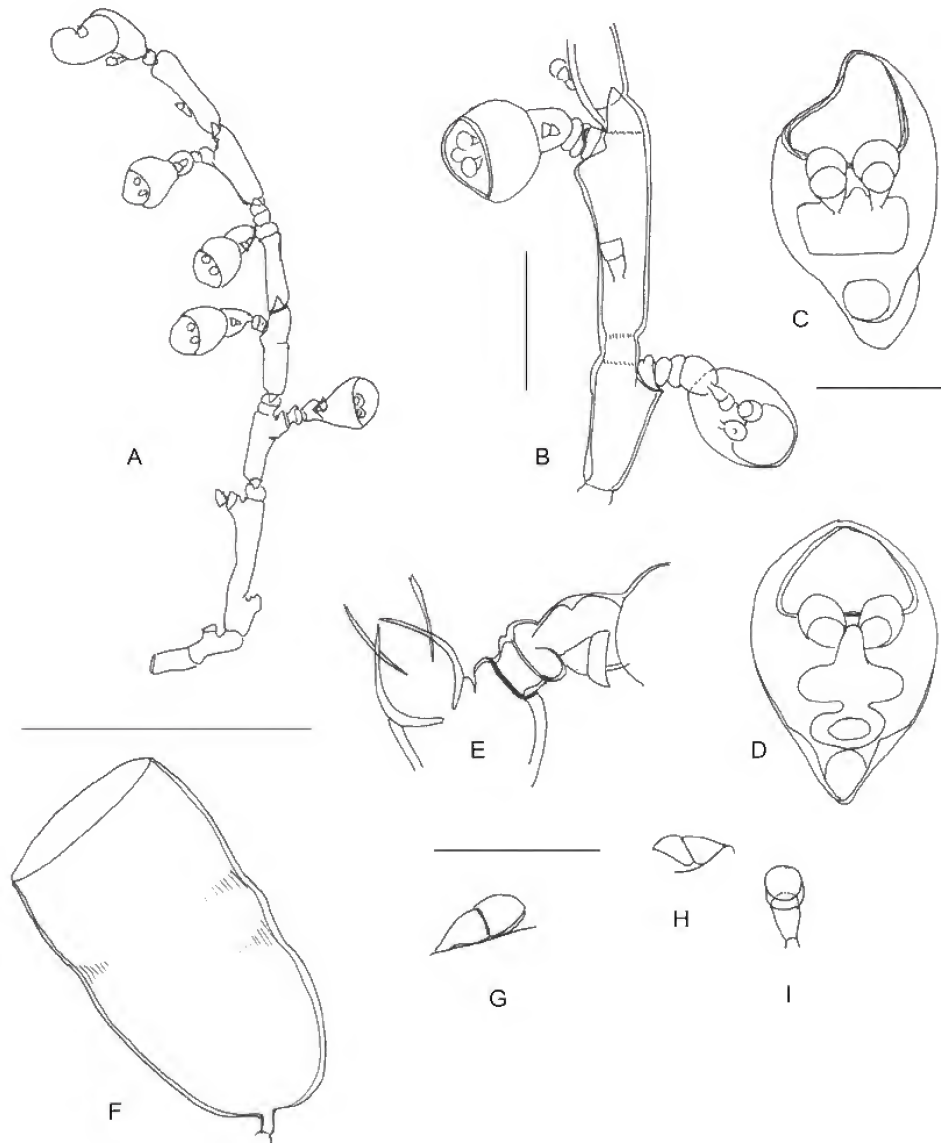


Figure 6. A–I, *Monotheca togata*. A, stem; B, part of stem showing internodes; C, slightly oblique ventral view of hydrotheca; D, full ventral view of hydrotheca, both views showing twin lateral nematothecae; E, apophysis of stem with proximal hydrocladium; F, gonotheca; G, cauline nematotheca; H, median inferior nematotheca; I, one of twin lateral nematothecae. Scale bar: A, F, 1 mm; B, 0.3 mm; C–I, 0.1 mm.

beside apophysis on first stem internode, body barrel shaped, distally truncated, walls smooth to weakly undulated, aperture terminal, transverse, closed by a sheet of tissue. Female gonotheca unknown.

***Monothecha togata*, measurements (μm)**

Hydrorhiza, width	72–80
Stem	
length of cauline internode	300–360
width at subnodal septum	76–80
length of apophysis (adcauline)	40–50
Hydrocladium	
length of subhydrothecal chamber adcauline	100–130
length of athecate internode	30–40
width at distal shoulder	44–64
length of hydrothecate internode (along base)	180–220
Hydrotheca	
depth, floor to highest point on margin	192–224
width across margin (frontal view)	186–200
Nematotheca	
length of base of cauline	36–52
width of cup	26–40
length of base of median inferior	28–32
width of cup	48–52
width of cup of lateral	30–44
Gonotheca	
length of pedicel	35–40
length excluding pedicel	1040–1260
distal diameter	600

Remarks. The cauline and axillar nematothecae are often absent. The frontal position of the cauline apophysis causes the hydrocladia and hydrothecae to twist forward during microslide mounting, which tends to obscure some structures.

This is first description of the gonotheca of *Monothecha togata*. The species is closely related to *M. hyalina* in size of stems and the cowl-shaped hydrotheca with a hemispherical margin. The distinctive adcauline apertural peak of *M. togata* distinguishes it from *M. hyalina*.

Monothecha togata (NMNZ BS834), was reported from East Cape and Ranfurly Bank, New Zealand, by Vervoort and Watson (2003). However, the material differs from the Australian species in having i) no axial hydrostatic pore, ii) a much smaller hydrocladial median inferior nematotheca, and iii) shorter cauline and hydrothecate internodes. In contrast to the epiphytic Australian species, the New Zealand material is epizootic on *Syntheicum suventricosum* and *Halopteris campanula*. These structural and substrate preferences may indicate the New Zealand material is a different species, but until more is known, the material is here doubtfully referred to *M. togata*.

Type locality. Pearson Island, Great Australian Bight.

Known distribution. Southern Australia to Western Australia, ?New Zealand.

Key to species of *Monothecha* in Australia

- 1 Hydrotheca cup or bowl shaped 3
- hydrotheca not this shape 2
- 2 Hydrotheca scoop, cowl or hood shaped 6
- 3 Hydrotheca with conspicuous abcauline flange
..... *Monothecha amphibola*
- hydrotheca with inconspicuous abcauline flange or no flange 4
- 4 Hydrocaulus flexuous, gonotheca barrel shaped with distal aperture *Monothecha flexuosa*
- hydrocaulus robust, gonotheca not barrel shaped 5
- 5 Aperture of gonotheca oblique with submarginal lobes
..... *Monothecha pulchella*
- 6 Hydrotheca with adcauline intrathecal septum 7
- hydrotheca without intrathecal septum 9
- 7 Intrathecal septum inconspicuous *Monothecha obliqua*
- intrathecal septum well developed 8
- 8 Hydrocladium with terminal spine
..... *Monothecha spinulosa*
- hydrocladium without terminal spine
..... *Monothecha australis*
- 9 Hydrotheca subhemisphaerical, margin hooded 10
- 10 Hydrotheca with distinct adcauline marginal peak
..... *Monothecha togata*
- 11 Hydrothecal margin without adcauline peak
..... *Monothecha hyalina*

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References

- Anonymous 2004. Catalogues of the collections in the Showa Memorial Institute, National Science Museum, Tokyo. No. 2: 1–139.
- Bale, W. M. 1882. On the Hydroids of south-eastern Australia, with descriptions of supposed new species, and notes on the genus *Aglaophenia*. *Journal of the Microscopical Society of Victoria* 2: 15–48, pls 12–15.
- Bale, W. M. 1884. *Catalogue of the Australian hydroid zoophytes*. Australian Museum, Sydney. Pp. 198, pls 1–19.
- Bale, W. M. 1888. Some new and rare hydroids in the Australian Museum. *Proceedings of the Linnean Society of New South Wales*: 745–799.

- Bale, W. M. 1894. Further notes on Australian hydroids, with descriptions of some new species. *Proceedings of the Royal Society of Victoria* (n.s.) 6: 93–117, pls 3–6.
- Bartlett, G. C. 1907. Notes on hydroid zoophytes. *Geelong Naturalist* 3: 35–45, 60–66.
- Bedot, M. 1921. Notes systématiques sur les plumularides. 1re partie, *Revue Suisse de Zoologie* 28: 311–356.
- Berrisford, C. D. 1968. Biology and zoogeography of the VEMA Seamount: a report on the first biological collection made on the summit. *Transactions of the Royal Society of South Africa* 38(4): 387–398.
- Billard, A. 1927. Les Hydroides de la côte atlantique de France. *Compte Rendu du Congrès des Sociétés Savantes de Paris et des Départements. Sections des Sciences*, 1926: 326–346.
- Billard, A. 1936. Les fonds de pêche près d'Alexandre VI. Hydroides. *Notes et Mémoires du Ministère de Commerce et de l'Industrie d'Egypte* 73: 1–11.
- Blackburn, M. 1937. Notes on Australian Hydrozoa, with descriptions of two new species. *Proceedings of the Royal Society of Victoria* 50: 170–181.
- Blackburn, M. 1938. Hydrozoa. The Sir Joseph Banks Islands. Reports of the expedition of the McCoy Society for field investigation and research, 3. *Proceedings of the Royal Society of Victoria* 50: 312–328.
- Blackburn, M. 1942. A systematic list of the Hydroida of South Australia with a summary of their distribution in other seas. *Transactions of the Royal Society of South Australia* 66: 104–118.
- Blanco, O. M. 1973. Nuevos plumularidos para aguas Argentinas. *Neotropica. Notas Zoológicas Sudamericanas* 19: 73–78.
- Boero, F. 1981a. Systematics and ecology of the hydroid population of two *Posidonia oceanica* meadows. *Pubblicazione della Stazione Zoologica di Napoli. Marine Ecology* 2: 181–197.
- Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. *Pubblicazione della Stazione Zoologica di Napoli. Marine Ecology* 5: 93–118.
- Boero, F., Chessa, L., Chimez, C. and Fresi, E. 1985. The zonation of epiphytic hydroids on the leaves of some *Posidonia oceanica* (L.) Delile beds in the central Mediterranean. *Pubblicazione della Stazione Zoologica di Napoli. Marine Ecology* 6: 27–33.
- Gili, J.-M., W. Vervoort and Pagès, F. 1989. Hydroids from the west African coast: Guinea Bissau, Namibia and South Africa. *Scientia Marina* 53(1): 67–112.
- Bouillon, J., Massin, C. and Krešević, R. 1995. Hydroidomedusae de l'Institut Royal des Sciences naturelles de Belgique. *Documents de Travail de l'Institut Royal des Sciences Naturelles de Belgique* 78: 3–106.
- Bouillon, J., Medel, M. D., Pagès, F., Gili, J.-M., Boero, F. and Gravili, C. 2004. Fauna of the Mediterranean. Hydrozoa. *Scientia Marina* 68(2): 5–438.
- Bouillon, J., Gravili, C., Pagès, F., Gili, J.-M. and Boero, F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1–591.
- Briggs, E.A. 1918. Descriptions of two new hydroids and a revision of the hydroid-fauna of Lord Howe Island. *Records of the Australian Museum* 12: 27–47, pls 5–6.
- Broch, H. 1933. Zur Kenntnis der Adriatischen Hydroidenfauna von Split. Arten und Variationen. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo. Mat.-Nat. Klasse* 1933(4): 1–115.
- Calder, D. R. 1997. Shallow-water hydroids of Bermuda: (Superfamily Plumularioidea). *Royal Ontario Museum Life Science Contributions* 161: 1–86.
- Cornelius, P.F.S. 1995. North-west European thecate hydroids and their medusae. Part 2. Sertulariidae to Campanulariidae. in: Barnes, R.S.K. and Crothers, J.H. (eds). *Synopses of the British fauna (new series)* 50: 1–386.
- Day, J. H., Millard, N. A. H. and Harrison, A. D. 1952. The ecology of South African estuaries. *Transactions of the Royal Society of South Africa* 33: 367–413.
- Day, J. H., Field, J. G. and Penrith, M. J. 1970. The benthic fauna and fishes of False Bay, South Africa. *Transactions of the Royal Society of South Africa* 39: 1–108.
- El Beshbeeshy, M. 1995. Systematische, Morphologische und Zoogeographische Untersuchungen an den Thekaten Hydroiden des Patagonischen Schelfs. Dissertation, Universität Hamburg. Pp 1–390.
- Fresi, E., Chimez, C. and Marchio, G. 1982. Zonazione di briozoi ed idrioidi epifiti in una prateria di *Posidonia oceanica* (L.) Delile. *Naturaliste Sicily* 6: 499–508.
- García-Corrales, P., Aguirre Inchaurre, A. and Gonzalez Mora, D. 1978. Contribución al conocimiento de los hidrozoo de las costas españolas. Parte I: Halécidos, campanuláridos y plumuláridos. *Boletín del Instituto Español de Oceanografía* 4(253): 5–73.
- Genzano, G. N. 1990. Hidropólipos (Cnidaria) de Mar del Plata, Argentina. *Nerítica* 5(1): 50–52.
- Genzano, G. N. 1994. Organismos epizóicos de *Amphisbetia operculata* (L) (Cnidaria, Hydrozoa). *Iheringia, Zoologica* 76: 3–8.
- Hirohito 1974. Some hydroids of the Bonin Islands. *Publications of the Biological Laboratory, Imperial Household, Tokyo* 1974: 1–55, figs 1–20.
- Hirohito, 1983. Hydroids from Izu Oshima and Nijima. *Publications of the Biological Laboratory, Imperial Household, Tokyo* (1983)6: 1–83, figs 1–41.
- Hirohito, 1995. The hydroids of Sagami Bay. II. *Publications of the Biological Laboratory, Imperial Household, Tokyo* 1995: 1–244, pls 1–13.
- Hodgson, M. M. 1950. A revision of the Tasmanian Hydroida. *Papers and Proceedings of the Royal Society of Tasmania* 1949: 1–65.
- Isasi, I. and Saiz, J.I. 1986. Sistemática de Cnidarios del Abra de Bilbao. *Cuadernos de Investigaciones Biológicas* 9: 67–74.
- Izquierdo, M. S., García-Corrales, P. and Bacallado, J. J. 1986. Contribution to the study of the calyptoblastid hydrozoans of the Canary Islands (Spain). II. Plumulariidae. *Boletín del Instituto Español de Oceanografía* 3(2): 49–66.
- Jäderholm, E. 1919. Zur Kenntnis der Hydroidenfauna Japans. *Arkiv för Zoologi* 12(9): 1–34, pls 1–6.
- Johnston, G. 1847. A History of the British Hydroid Zoophytes. Van Voorst, London, 2nd edition. Vol. 1 : i–xvi, 1–488, figs 1–87; vol. 2 : pls 1–74.
- Kirchenpauer, G.H. 1876. Ueber der Hydroidenfamilie Plumulariidae, einzelne Gruppe derselben und ihre Fruchthälter. II. *Plumularia* und *Nemertesia*. *Abhandlungen aus dem Gebiete der Naturwissenschaften*, Hamburg 6: 1–59, pls 1–8.
- Leclère, L., Schuchert, P. and Manuel, M. 2007. Phylogeny of the Plumularioidea (Hydrozoa, Leptothecata): evolution of colonial organisation and life cycle. *Zoologica Scripta* 36: 371–394.
- Leloup, E. 1932. Une collection d'hydropolypes appartenant à l'Indian Museum de Calcutta. *Records of the Indian Museum* 34: 131–170.
- Leloup, E. 1934. Note sur les hydropolypes de la rade de Villefranche-sur-Mer (France). *Bulletin du Muséum Royal d'Histoire Naturelle de Belgique* 10: 1–18.
- McCrary, J. 1859. Gymnophthalma of Charleston Harbor. *Proceedings of the Elliot Society of Natural History of Charleston, South-Carolina* 1: 105–221.

- Medel, M. D. and López-González, P. J. 1996. Updated catalogue of the Iberian Peninsula and Balearic Islands, with remarks on zoogeography and affinities. *Scientia Marina* 60(1): 183–189.
- Medel, M. D. and Vervoort, W. 1995. Plumularian hydroids (Cnidaria: Hydrozoa) from the Strait of Gibraltar and nearby areas. *Zoologische Verhandelingen, Leiden*, 300: 11–72.
- Millard, N. A. H. 1957. The Hydrozoa of False Bay, South Africa. *Annals of the South African Museum* 43: 173–243.
- Millard, N.A.H. 1962. Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae. *Annals of the South African Museum* 46: 261–319.
- Millard, N.A.H. 1966. The Hydrozoa of the south and west coasts of South Africa. Part III. The Gymnoblastea and small families of the Calyptoblastea. *Annals of the South African Museum* 48: 427–487.
- Millard, N. A. H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1–513.
- Millard, N. A. H. 1978. The geographical distribution of southern African hydroids. *Annals of the South African Museum* 74: 159–200.
- Millard, N. A. H. 1980. Hydroida. The South African Museum's *Meiring Naude* cruises. Part II. *Annals of the South African Museum* 82: 129–153.
- Millard N.A.H. and Bouillon, J. 1974. A collection of hydroids from Moçambique, East Africa. *Annals of the South African Museum* 65: 1–40, figs 1–9.
- Mulder, J. F. and Trebilcock, R. E. 1910. Notes on Victorian hydroids with descriptions of new species. *Geelong Naturalist* 4(2): 115–120.
- Mulder J. F. and Trebilcock, R. E. 1915. Victorian Hydroida with description of new species. Part V. *Geelong Naturalist* 6(3): 51–59, pls 7–9.
- Mulder J. F. and Trebilcock, R. E. 1916. Notes on Victorian Hydroida. Part VI. *Geelong Naturalist* 6(4): 73–84, pls 10–11.
- Nutting, C.C. 1900. American hydroids. Part I. The Plumulariidae. *Special Bulletin of the United States Museum* 4(1): 1–285, pls 1–34.
- Park, J.H. 1992. Zoogeographical distribution of marine hydroids (Cnidaria: Hydrozoa: Hydroida). *Korean Journal of Systematic Zoology* 8(2): 279–300.
- Pennycuik, P. R. 1959. Faunistic records from Queensland. Part V. Marine and brackish water hydroids. *Papers of the Department of Zoology, University of Queensland* 1: 141–210.
- Ralph, P. M. 1961b. New Zealand thecate hydroids. Part IV. The family Plumulariidae. *Transactions of the Royal Society of New Zealand, Zoology* 1: 19–74.
- Ralph, P. M. 1961c. New Zealand thecate hydroids. Part V. The distribution of the New Zealand thecate hydroids. *Transactions of the Royal Society of New Zealand, Zoology* 1: 103–111.
- Rho, B. J. and Park, J. L. 1986. A systematic study on the marine hydroids in Korea. 8. On two new species belonging to the family Plumulariidae. *Korean Journal of Zoology* 217: 255–263.
- Roca, I. 1987. Hydroids on Posidonia in Majorcan waters. Pp 209–214 in: Bouillon, J., Cicogna, F., Cornelius P.F.S. (eds). *Modern trends in the systematics, ecology and evolution of hydroids and hydromedusae*. Clarendon Press, Oxford.
- Rossi, I. 1950. Celenterati de Golfe di Rapallo (Rivieri Ligure). *Bolletino dell'Instituto e Museo di Zoologia della Università di Torino* 2: 193–235.
- Ryland, J.S. and Gibbons, M.J. 1991. Intertidal and shallow water hydroids from Fiji. II. Plumulariidae and Aglaopheniidae. *Memoirs of the Queensland Museum* 30: 525–560.
- Shepherd, S.A. and Watson, J.E. 1970. The Sublittoral ecology of West Island, South Australia. 2. The association between hydroids and algal substrate. *Transactions of the Royal Society of South Australia* 94: 139–146, pl. 1.
- Staples, D. A. and Watson, J. E. 1987. Associations between pycnogonids and hydroids. Pp. 215–226 in: J. Bouillon, F. Boero, F. Cicogna and Cornelius, P. F. S. (eds), *Modern trends in the systematics, ecology and evolution of hydroids and hydromedusae*, Clarendon Press, Oxford.
- Stechow, E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologischer Jahrbücher, Abteilung für Systematik* 42: 1–172.
- Stechow, E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertabraten. *Archiv für Naturgeschichte* 87: 248–265.
- Stechow, E. 1923a. Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andre Formen. *Zoologischer Anzeiger* 56: 1–20.
- Stechow, E. 1923b. Die Hydroidenfauna der japanischen Region. *Journal of the Imperial University of Tokyo* 44: 1–23.
- Stechow, E. 1923d. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zoologischer Jahrbücher, Abteilung für Systematik* 47: 29–270.
- Stechow, E. 1924. Diagnosen neuer Hydroiden aus Australien. *Zoologischer Anzeiger* 59: 57–69.
- Stechow, E. 1925. Hydroiden von West- und Südwestaustralien nach den Sammlungen von Prof. Dr. Michaelsen und Prof. Dr. Hartmeyer. *Zoologische Jahrbücher, Abteilung für Systematik* 50: 191–270.
- Totton, A.K. 1930. Coelenterata. Part V. Hydroida. *Natural History Report. British Antarctic Terra Nova Expedition 1910, Zoology* 5(5): 131–252, pls 1–3.
- Stranks, T. N. 1993. Catalogue of recent cnidarian type specimens in the Museum of Victoria. *Occasional Papers from the Museum of Victoria* 6: 1–26.
- Trebilcock, R. E. T. 1928. Notes on New Zealand Hydroida. *Proceedings of the Royal Society of Victoria* n. ser. 41(1): 1–31.
- Vervoort, W. and Watson, J. E. 2003. Marine fauna of New Zealand. Leptothecata (Cnidaria: Hydrozoa) (Thecate Hydroids) *NIWA Biodiversity Memoir* 119: 1–538.
- Von Lendenfeld, R. 1885a. The Australian Hydromedusae. *Proceedings of the Linnaean Society of New South Wales* 9: 206–241, 345–353, 401–420, 467–492, 581–634, pls 6–8, 12–17, 20–29.
- Warren, E. 1908. On a collection of hydroids mostly from the Natal coast. *Annals of the Natal Museum* 1: 269–355.
- Watson, J. E. 1973. Hydroids. Pearson Island expedition 9. *Transactions of the Royal Society of South Australia* 97: 153–200.
- Watson, J. E. 1975. Hydroids of Bruny Island, southern Tasmania. *Transactions of the Royal Society of South Australia* 99: 157–176.
- Watson, J.E. 1979. Biota of a temperate shallow water reef. *Proceedings of the Linnaean Society of New South Wales* 103: 227–235.
- Watson, J.E. 1982. Hydroids (Class Hydrozoa). Pp 77–115 in: Shepherd, S.A. and Thomas I.M (eds) *Handbook of the flora and fauna of South Australia. Marine invertebrates of southern Australia 1*. Handbook Committee, South Australian Government, Adelaide.
- Watson, J. E. 1992. The hydroid community of *Amphibolis* seagrasses in south-eastern and south-western Australia. in: J. Bouillon, F. Boero, F. Cicogna, J.-M. Gili and Hughes, R. G. (eds), *Aspects of Hydrozoan Biology, Scientia Marina*. 56: 217–227.
- Watson, J. E. 1996. Distribution and biogeographic relationships of the hydroid fauna of the Australian west coast: a preliminary account. in: S. Piraino, F. Boero, J. Bouillon, P. F. S. Cornelius and Gili, J. M. (eds), *Advances in Hydrozoan Biology, Scientia Marina*. 60: 75–83.

- Watson, J. E. 1997. The hydroid fauna of the Houtman Abrolhos Islands, Western Australia. Pp. 503–546 in: F. E. Wells (ed.), *Proceedings of the Seventh International Marine Biological Workshop. The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*, Western Australian Museum, Perth.
- Watson, J.E. 2000. Hydroids (Hydrozoa) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 16: 1–82.
- Watson, J. E. 2003. Encounter 2002 expedition to the Isles of St Francis, South Australia: annotated list of shallow water hydroids with description of a new species of *Campanularia*. *Transactions of the Royal Society of South Australia* 127: 243–263.
- Watson, J. E. 2005. Hydroids of the Archipelago of the Recherche and Esperance, Western Australia: annotated list, redescription of species and description of new species. Pp 495–611 in: F.E. Wells, G.I Walker, and Kendrick, G.A. (eds). *The marine flora and fauna of Esperance, Western Australia*. Western Museum, Perth.
- Watson, J. E. and McInnes, D. E. 1999. Hydroids from Ricketts Point and Black Rock, Victoria. *The Victorian Naturalist* 116: 102–111.
- Yamada, M. 1959. Hydroid fauna of Japan and its adjacent waters. *Publications from the Akkeshi Marine Biological Station* 9: 1–101.

